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THE ORNITHISCHIAN DINOSAUR *HYPSILOPHODON* FROM THE WEALDEN OF THE ISLE OF WIGHT

By PETER MALCOLM GALTON

CONTENTS

SYNOPSIS

The anatomy of the primitive ornithopod *Hypsilophodon* is described. The femur described as *Camptosaurus valdensis* is referred to *Hypsilophodon foxii.* The skull was possibly mesokinetic, metakinetic and amphistylic. The large antorbital fenestra was enclosed to a varying extent in lower ornithopods to form a fossa for the M. pterygoideus. The jaw musculature was typically sauropsid, the coronoid process is large and the jaw articulation offset. The mouth was probably small with a cheek pouch lateral to the tooth rows. The teeth had sharp and serrated leading edges and oblique but parallel occlusal surfaces with a high shear component between them. There is a large amount of individual variation and the sacral count varies. The massive first sacral rib strengthened the slender pubic peduncle of the ilium and keyed the pubis to it. *Hypsilophodon* was definitely bipedal but probably ran with the vertebral column held horizontally. The structure of the phalanges of the pes is not unique and the hallux was

not opposable. *Hypsilophodon* was the most cursorial of the known post-Triassic ornithopods and it was not arboreal. *Hypsilophodon* was probably not directly ancestral to any Cretaceous ornithischian but structurally it is quite similar to the hypothetical Triassic ancestor of most ornithischians other than *Fabrosaurus*.

I. INTRODUCTION

A slab of sandstone containing the partial skeleton of a reptile was discovered in 1849 at the top of the Wealden Marls near Cowleaze Chine, on the south-west coast of the Isle of Wight, England. Mantell (1849) figured and described three cervical vertebrae from this specimen as those of a very young *Iguanodon*. Owen (1855) illustrated the complete block and described it as belonging to a young *Iguanodon mantelli*. Fox exhibited more material from this same Wealden bed at the British Association meeting at Norwich in 1868. This included a skull and various post-cranial remains, which he identified as a new species of *Iguanodon* (Fox 1869). Huxley (1870, abstract 1869) described and figured this skull, making it the type of a new genus and species, *Hypsilophodon foxii*. He showed that a centrum from a dorsal vertebra on this specimen was identical to those described by Owen, and he therefore suggested that Owen's skeleton too belonged to *Hypsilophodon*. Huxley separated *Hypsilophodon* from *Iguanodon* by differences in the teeth, vertebrae and femur and in the number of metatarsals. He showed the parallel position of the pubis and ischium and the obtuse angle between these two bones and the anterior part of the ilium, the first time that this typically ornithischian condition had been shown.

In 1873 Hulke collected some additional material that formed the basis of two papers (1873, 1874); the first dealt mainly with the teeth and appendicular skeleton and the second with the skull. He noted that *Hypsilophodon* differed from *Iguanodon* in having four metatarsals, in the shape of the unguals, in having longer phalanges in the hind foot, a tibia longer than the femur and in the more proximal position of the inner (fourth) trochanter of the femur. In the discussion following Hulke (1873), Owen denied the generic separation of *Hypsilophodon* and referred to it as *Iguanodon foxii*. He stated that generic identity was shown by the similarity in tooth shape and wear, with the enamel layer on opposite sides in the upper and lower jaws, and by the peculiar spout-like form of the edentulous anterior end of the mandible. Owen (1874) elaborated these points when he described the skull of *Hypsilophodon* as that of *Iguanodon foxii*. Hulke (1882), in his attempt at a complete osteology, figured most of the important material and described the individual elements.

Lydekker (1888) catalogued the material of *Hypsilophodon* in the British Museum (Natural History). Nopcsa (1905) discussed certain aspects of the anatomy while von Huene (1907) figured the ilium and ischium. Abel in 1911 reconstructed the forearm and hand, and the foot in 1912. He argued (1912, 1922, 1925, 1927) that *Hypsilophodon* was arboreal, a conclusion that was followed and expanded by Heilmann (1916) and Swinton (1934, 1936*a*, *b*) although Heilmann later (1926) disagreed.

Reconstructions and restorations of *Hypsilophodon* are given by Hulke (1882), Smit (in Hutchinson 1894), Marsh (1895, 1896*a*, *b*), Heilmann (1916), Abel (1922 and later), von Huene (1956), Wilson (in Oakley & Muir-Wood 1959), Ostrom (1964) and Colbert (1965). General accounts are given in Swinton (1934, 1936*a*, *b*, 1954, 1962) and with one exception (1936*b*) these are accompanied by restorations. He also (1936) described the maxilla, teeth, pectoral girdle and limbs from two fairly complete skeletons in the Hooley Collection acquired by the British Museum (Natural History). Mounts were made of these two skeletons, photographs of which were published by Swinton (1934, 1936*a*).

Because of its primitive structure and supposedly arboreal mode of life, *Hypsilophodon* is an especially interesting dinosaur and, as indicated above, it has been the subject of numerous papers. However, the available account of its anatomy is still far from complete despite the fact that it is the best represented British dinosaur. This paper is the result of further preparation and study of the specimens available ; there are twenty individuals represented by articulated bones, including one almost complete skeleton and two good skulls. The study of the pelvic musculature of *Hypsilophodon*, with a consideration of the functional significance of the prepubic process of ornithischians, has already been published (Galton 1969). The mode of life of *Hypsilophodon* has also been discussed elsewhere (see p. 149).

II. MATERIAL AND METHODS

a) *Preparation*

Apart from the material noted on page 10 all the remains of *Hypsilophodon* are in the British Museum (Natural History) and the appropriate specimen numbers are used in this paper. With the exception of R5829 and R5830 all articulated remains were in blocks with the bones exposed on the surface. The slab (28707) figured by Owen (1855) has been left unprepared to show the original appearance of these blocks. Hulke (1882) figured all the other important blocks ; these were developed further so that now, in most cases, the bones are completely free of matrix. Mechanical preparation was used on most of the material. The matrix of blocks with articulated remains was a hard sandstone which prepared well in 10 per cent acetic acid, following the methods developed by Toombs (1948) and Rixon (1949). Polybutyl methacrylate dissolved in methylethyl ketone was used to strengthen and harden the bone, with Glyptal as an adhesive. Acid preparation was used on R193, R195, R196, R197, R198, R200 and R2477.

b) *Material*

There are many isolated bones of *Hypsilophodon* in the British Museum (Natural History) collection but most are incomplete and badly preserved. Details of all the material are listed by Galton (1967). Diagrams showing the amount of each bone preserved in specimens 28707, R192, R193, R195, R196, R200, R2466–76, R2477, S.M. 4127, R5829 and R5830 are given as well as a table listing all the skull bones in the collection (Galton 1967, figs. 5–18). The following list contains only specimens referred to in the literature or in this paper and the author and plate or figure numbers are given. For details of the actual bones figured reference should be made to Section (c) in which all previous figures are listed with the relevant specimen numbers (not given in papers prior to 1936) and an indication of the bones concerned.

Mantell Collection, purchased 1853

28707, 39560–1. This specimen will be referred to as 28707 and is the paratype (Huxley 1869). Slab of sandstone with an articulated skeleton consisting of a partial vertebral column, pelvic region and hindlimbs. Found in cliff about 100 yd west of Cowleaze Chine, Isle of Wight (Owen 1855 : 2). Figured by Mantell (1849, pl. 29, fig. 9*), Owen (1855, pl. 1 – complete block ; pl. 15, fig. 8), Huxley (1870, pl. 1, figs. 6–8 ; pl. 2) and Hulke (1882, pl. 74, figs. 1–4).

36509. Distal end of right femur, matrix a soft red sandstone, from Cuckfield, Sussex. This specimen was referred to *Hypsilophodon* by Lydekker (1888) and was the only specimen not from the Isle of Wight. However, this femur has a deep anterior intercondylar groove, and is therefore not referable to *Hypsilophodon* (see Text-fig. 54) ; this means that the genus has not been found outside the Isle of Wight.

Fox Collection, purchased 1882

R167. Large left femur, ends imperfect (Pl. 2, fig. 4), referred by Lydekker (1888) to *Hypsilophodon* but subsequently (1889) made the type of *Camptosaurus valdensis.* The generic position of this specimen is discussed in Section V.

R170. Left tibia, listed by Lydekker (1888) as right but corrected later (1891). The 1888 catalogue also lists under *Iguanodon* for this number 'Three specimens of the distal extremity of the humerus of very young individuals'. Material actually consists of a distal end of a left tibia, two proximal and two distal ends of femora, distal end of a humerus and a distal end of the third metatarsal – all *Hypsilophodon.*

R183. An ulna of *Hypsilophodon* according to Lydekker (1888) ; but actually the fourth right metatarsal of an ornithopod.

R184, R185. Associated pair of femora listed by Lydekker (1888). These are ornithopod but not *Hypsilophodon.*

R186. Right tibia, listed by Lydekker (1888) as a left tibia which was apparently associated with the femora R184 and R185. Corrected to right tibia when Lydekker (1891) referred it to the coelurosaur *Calamospondylus foxi* ; R186 was obviously not from the same animal as the femora !

R189. Part of right ramus of mandible found about 210 yd east of Barnes High (Fox in letter quoted by Owen 1874 : 13). Figured by Owen (1874 : 2, figs. 8–11).

R190. Right mandibular ramus, two caudal vertebrae and parts of ribs on a sandstone slab. Found about 150 yd east of Barnes High (Fox, letter quoted by Owen 1874 : 13). Figured by Owen (1874, figs. 1–2).

R191. Tooth from R190 figured by Owen (1874, pl. 2, figs. 12–17).

R192. Block with articulated bones of pectoral girdle, forelimbs, neck and jaws with various disarticulated skull bones of a large individual. Also other blocks with parts of pelvis and hind limbs ; all the bones are poorly preserved. From *Hypsilophodon* Bed (Fox MS) ; main block figured by Hulke (1882, pl. 73).

R192a. Large left femur that does not belong to same individual as R192 because latter already includes two femora. From *Hypsilophodon* Bed (Fox MS) ; figured by Hulke (1882, pl. 78, figs. 1–5).

R192b. Ilium and prepubic process from an extremely young individual.

R193. Block with articulated bones of pelvis, hindlimb and tail. From *Hypsilophodon* Bed ; figured by Hulke (1882, pl. 77), Galton (1969, figs. 4, 6–11, 13, 15) and Text-figs. 24, 25D, 26B, C, 30, 31, 49, 50, 53A, B and 55.

R194. Block with skull elements, right humerus and radius. From *Hypsilophodon* Bed (Fox MS) ; incorrectly listed by Lydekker (1888 : 194) as 'an imperfect pelvis and bones of the hind limb'. Figured by Hulke (1882, pl. 72, fig. 1) as an eroded internal aspect of skull but actually the external aspect. Partial basis for Text-fig. 9.

R195. Block with pelvic region from *Hypsilophodon* Bed (Fox MS). Figured by Hulke (1882, pl. 76) and Text-figs. 25A, B, E, F, 26A, 27, 46, 47 and 52.

R196, R196a. Two blocks (for photographs taken before preparation see Galton 1967, figs. 19–21) which together contained a practically complete articulated skeleton (R196) plus the posterior half of a tail from a larger individual (R196a) ; from *Hypsilophodon* Bed (Fox MS). R196 figured by Hulke (1882, pl. 72, fig. 2 ; pl. 74, fig. 13 ; pl. 75 and pl. 79, figs. 2–3), Nopcsa (1905, fig. 1), Abel (1911, fig. 12 ; 1912, fig. 12), Galton (1970, fig. 5B ; in press *a*, figs. 5A, B) and Text-figs. 12, 13, 19–23, 25C, 26D, 28, 29, 33–35, 37, 38, 40, 41, 48A, 51, 53C, D, 58 and Pl. 2, fig. 3 ; R196a by Hulke (1882, pl. 74, fig. 13) and in text-fig. 62.

R197. The holotype, a skull of a small individual plus a partial atlas, a cervical vertebra and a dorsal centrum. Found about 210 yd east of Barnes High (Fox in letter quoted by Owen 1874 : 13). Figured by Huxley (1870, figs. 1–5), Owen (1874, pl. 1, figs. 9–10 ; pl. 2, figs. 1, 5), Hulke (1882, pl. 71, figs. 2–4) and in Text-fig. 2.

R199. Left tibia of large individual, listed as right by Lydekker (1888) but later corrected (1891). From *Hypsilophodon* Bed (Fox MS) ; figured by Hulke (1882, pl. 80, fig. 2 ; pl. 81, fig. 1).

R200. Left and right hind-feet of large animal(s) from *Hypsilophodon* Bed (Fox MS). These two feet are about the same size and the matrix is very similar but they may be from different animals as they were given separate find numbers – IJ (right) and IL in Fox (MS) ; figured by Hulke (1882, pl. 81, figs. 2–3).

R202a. Imperfect dorsal vertebra listed by Lydekker (1888).

R752. Right tibia, listed by Lydekker (1888) as a left tibia but later (1891) corrected.

R8422. Sacral centra 1, 2 and 3 from a large individual, damaged, no data.

Hulke Collection, purchased 1895

R2466–R2476. Parts of one small individual in soft grey marl. Found in cliff about 100 yd west of Cowleaze Chine (Hulke MS : 40), not the west end of the Bed as stated by Hulke (1874 : 18). All this material was described by Hulke (1873) who figured some of it in that work (pl. 18, figs. 1–8) and again in 1882 (pl. 72, figs. 3–9 ; pl. 79, figs. 1, 4) ; Nopcsa (1905, fig. 3) figured the only known predentary, which is also shown in Text-fig. 11.

R2477. Block which contained a skull with atlas and axis, dermal armour and two vertebral series (a, b) each consisting of the posterior dorsals and the anterior sacrals. Found on the beach between Barnes High and Cowleaze Chine after it had been rolling about for some time (Hulke 1874). Figured by Hulke in 1874 (pl. 3, figs. 1, 2) and 1882 (pl. 71, fig. 1 ; pl. 76, fig. 2) as well as by Nopcsa (1905, figs. 2, 4). Photographs showing the complete block before preparation plus the lateral and dorsal views of the skull in the round are given by Galton (1967, figs. 22–25). The skull is shown in Text-figs. 4–8, 12, 17, 60, 61, Pl. 1, and Pl. 2, figs. 1, 2 ; the atlas and axis in Text-fig. 18 ; skull also in Galton (in press figs. 6–8).

R2481. Twelve centra and one complete cervical vertebra found near Cowleaze Chine (Hulke MS). Figured by Hulke (1882, pl. 74, figs. 5–8).

Hooley Collection, purchased 1924

R5829. Nearly complete mounted skeleton (see Swinton 1936*a*, fig. 2) of a large individual ; bones slightly crushed. Found near Cowleaze Chine (Register B.M. (N.H.) Collection and on card with Hooley Collection) and not from the Chine itself as stated by Swinton (1936), who gives measurements and descriptions of some of these bones.

R5830. Nearly complete mounted skeleton (see Swinton 1934, pl. 23 ; 1936*a*, fig. 2) of a small individual ; bones show practically no distortion, articular surfaces are well preserved. Locality data as for R5829 ; bones figured by Swinton (1936, figs. 4–7) and in Text-figs. 32, 36, 39, 42–45, 53E, 54, 56 and 57.

The manus as mounted contained phalanges of a pes but, because the hind-feet are already complete, these extra pedal elements must belong to a second individual. In the Hooley Collection there are several bones from a small individual (see Galton 1967, fig. 17) of which the state of preservation closely resembles that of R5830 ; some of these correspond to elements which are missing from the mounted skeleton and probably belong to it, others duplicate elements from the mounted skeleton (see Galton 1967, fig. 16) and must belong to other individuals. All this material is numbered R5830.

R5862. Left maxilla from near Cowleaze Chine (Register B.M. (N.H.) Collection), figured by Swinton (1936, fig. 1).

R5863. Part of left mandible from near Cowleaze Chine (Register B.M. (N.H.) Collection) ; teeth figured by Swinton (1936, figs. 2, 3).

R6372. Intercentrum of atlas described by Swinton (1936) and five jaw fragments ; from Cowleaze Chine (Register B.M. (N.H.) Collection).

R8367. Isolated skull bones, no data ; isolated teeth, see Text-figs. 14–16.

R8419. Right exoccipital and paroccipital process, no data, see Text-fig. 9.

Other material

R8352. Distal part of large right femur with fourth trochanter, found near Cowleaze Chine in the early 1960's.

R8366. Many isolated bones from at least two individuals, one small and the other medium-sized ; discovered about 100 m west of Cowleaze Chine in September, 1965 by a field party from the 13th Symposium on Vertebrate Palaeontology and Comparative Anatomy.

R8418. Skull elements and teeth from the above find, partial basis for Text-fig. 9.

Museum of the Geology of the Isle of Wight, Sandown, I.o.W. : Poole Collection, donated 1938 – **S.M. 4127.** Part of tail and hind-limb from Cowleaze Chine, basis for metatarsal V in Text-fig. 58 and for identification of distal tarsals in Text-fig. 57.

Department of Zoology, University College London : material found by a party led by Dr P. L. Robinson.

Vertebrae and limb bones from at least three small animals all found in a few cubic feet of the *Hypsilophodon* Bed. This material is badly preserved though much is in natural articulation. Photographs show that the locality was about 100 metres west of Cowleaze Chine in practically the same position as where R8366 was found.

c) *British Museum* (*Natural History*) *numbers of previously figured specimens*

Mantell, 1849	pl. 29, fig. 9*	28707	three cervical vertebrae
Owen, 1855	pl. 1,	28707	complete block
	pl. 15, fig. 8	28707	dermal armour (as integument)
Huxley, 1870	pl. 1, figs. 1–5	R197	skull and vertebra
	figs. 6–8	28707	caudal vertebra
	pl. 2	28707	pelvic region
Hulke, 1873	pl. 18, fig. 1	R2470	front part of dentary
	fig. 2	R2467	right scapula and coracoid
	fig. 3	R2473	part of manus
	fig. 4–7	R2471	teeth
	fig. 8	R2466	right foot
Hulke, 1874	pl. 3, fig. 1	R2477	skull and dermal armour
	fig. 2	R2477	two vertebral series a and b
Owen, 1874	pl. 1, figs. 9, 9a, 10	R197	skull
	pl. 2, figs. 1, 5	R197	skull
	figs. 8–11	R189	part of mandible

Owen, 1874	pl. 2,	figs. 12–17	R191	tooth
		text-fig. 1	R190	mandibular ramus
		fig. 2	R190	caudal vertebra
Hulke, 1882	pl. 71,	fig. 1	R2477	skull, palate
		figs. 2–4	R197	skull
	pl. 72,	fig. 1	R194	eroded skull
		fig. 2	R196	part of left mandible
		figs. 3–5	R2471	teeth
	pl. 73		R192	block with pectoral girdle, neck, jaws
	pl. 74,	figs. 1–4	28707	three cervical vertebrae
		figs. 5–8	R2481	cervical vertebra
		figs. 9–12		from Fox Collection but originals could not be found
		fig. 13	R196a	three caudal vertebrae
	pl. 75		R196	pelvic region
	pl. 76,	fig. 1	R195	pelvic region
		fig. 2	R2477	sacrum b
	pl. 77		R193	right pelvic bones and foot
	pl. 78,	figs. 1–5	R192a	left femur
		figs. 6–7		from Hulke Collection but originals could not be found
	pl. 79,	fig. 1	R2467	right scapula, coracoid, humerus
		figs. 2–3	R196	right fore-arm, left humerus
		fig. 4	R2466	left foot
	pl. 80,	fig. 1		from Hulke Collection but original could not be found
		fig. 2	R199	right tibia
		figs. 3–8		originals could not be found
	pl. 81,	fig. 1	R199	right tibia
		figs. 2–3	R200	right and left foot
Nopcsa, 1905		fig. 1	R196	braincase, occiput
		figs. 2, 4	R2477	occiput
		fig. 3	R2470	right dentary with predentary
von Huene, 1907		fig. 330	? R196	reconstruction of ilium
		fig. 331	R193	right ischium
Swinton, 1934	pl. 23		R5830	photograph of mounted skeleton
Swinton, 1936		fig. 1	R5862	left maxilla
		figs. 2–3	R5863	maxillary teeth

Swinton, 1936	figs. 4–7	R5830	scapula, coracoid, humerus, radius, ulna, tibia, fibula, astragalus, calcaneum
Swinton, 1936*a*	fig. 2	R5829 and R5830	photograph of the mounted skeletons
Galton, 1969	figs. 4, 6–11, 13, 15	all R193	figures and stereophotographs of pelvic girdle and femur to show areas of muscle attachment
Galton, in press	figs. 6–8	R2477	skull

Outline figures of the skull (R2477) and limb bones (R196) are given in Galton (1970*a*, 1971*a*, *b*, 1973, in press *a* ; see page 149).

d) *Measurements*

The proximal part of the femur gives the best indication of the relative size of important specimens. In Table I the measurement given is the minimum distance between the proximal end and the distal side of the base of the fourth trochanter (Text-fig. 1f). In specimens where no femur was available this distance was calculated by comparing other bones with specimens which have a femur ; the calculated values are given in parentheses. The total length of R5830 was about ·9 m, R196 about 1·36 m, R5829 about 1·8 m and R167 about 2·3 m. To facilitate comparison of the sizes of different bones from the same specimen all the measurements are given together in Tables II and III. Unless indicated to the contrary by a diagram in Text-fig. 1, L = greatest length, M_w = minimum width of shaft, W_d and W_p maximum width of distal and proximal ends. All measurements are in millimetres.

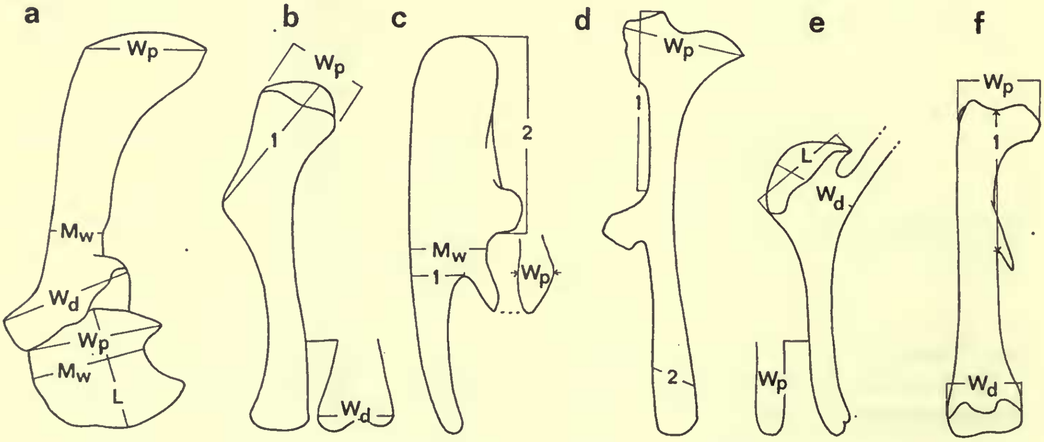


FIG. 1. Diagram to show the basis for some of the measurements in Tables I and II : a. scapula and coracoid ; b. humerus ; c. ilium ; d. ischium ; e. pubis ; f. femur.

TABLE I

To show the relative size of the specimens of *Hypsilophodon* – measurements in mm of fourth trochanter index of the femur, see Text-fig. 1f.

R5830	43	R196	65
R197	(49)	R192a	76
R2466-76	(55)	R200	(81)
S.M. 4127	(57)	R192	± 82
R2477 skull	(57)	R193	86
R2477a	± 60	R5829	87
R195	62	R167	108
28707	64		

TABLE II

Measurements of the bones of the girdles and the long limb bones
(All measurements in mm)

Bone	Spec. No.	L/R	L	Wp	Wd	Mw	1	2
Scapula	R5830	L	70·5	–	–	10	–	
(Text-fig. 1a)		R	(67·5)	24·5	25	–	–	
	R2467	R	88	32	26·5	12·5	–	
	R196	R	105	45	41	15	–	
	R192	R	+ 144	47	53	22	–	
	R5829	R	–	–	–	21	–	
Coracoid	R5830	R	20·5	–	–	–	–	
(Text-fig. 1a)	R2467	R	26	30	–	–	–	
	R196	L	35·5	43	–	35	–	
	R192	R	43	–	–	–	–	
Humerus	R5830	L	(74)	17	15	–	26	
(Text-fig. 1b)		R	69	16·5	14	6	–	
	R196	L	105	26·5	25	9·5	45·5	
		R	105	28	–	–	45·5	
	R192	L	147	+ 39	–	18	72	
	R5829	L	(159)	41	–	–	(64)	
		R	151	–	33	–	(68·5)	
Radius	R5830	L	–	9·5	–	4	–	
	R196	L	82·5	15(R)	13	6	–	
	R192	L	+ 111	–	–	8	–	
	R5829	R	114	–	–	–	–	
Ulna	R5830	L	–	8	–	–	9·5	–
	R196	L	88	11·5	14·5	6	19	–
	R192	L	± 125	–	–	11	25	–
Ilium	R195	R	–	11·5	–	21	15	–
(Text-fig. 1c)	R196	L	142	9	14	22	16	67
	R2477a	R	–	–	–	23	–	–
	R193	R	–	16	–	32	21	89(L)

TABLE II (*cont.*)

Bone	Spec. No.	L/R	L	Wp	Wd	Mw	1	2
Ischium	R5830	L	102	25·5	8·5	5·5	± 40	–
(Text-fig. 1d)	R195	L	–	36	–	8	60	14
	R196		–	46	–	9	–	21
	R193	R	–	49	–	14	79	28
	R5829	R	197	53	21	13·5	72	27
Pubis	R195	L	–	8	15	21·5	–	–
(Text-fig. 1e)	R196	R	–	10	–	–	–	–
	R193	R	38	14	–	–	–	–
	R5829	L	36	12	–	–	–	–
Femur								
(Text-fig. 1f)	R5830	L	101	26·5	25	10·5	43	–
	28707	L	± 150	–	–	–	64	–
	R196	L	± 150	–	–	14	65	–
	R192a	L	173	–	–	–	76	–
	R5829	R	202	–	56	–	–	–
		L	198	52	–	–	87	–
Tibia	R5830	R	117	26·5(L)	25·5	9		
	R196	R	–	–	40	–		
	SM4127	R	170	33	36	12		
	R193		–	58(L)	56·5(R)			
	R5829	L	238	(62)	45	17		
		R	(242)	(42)	–	–		

TABLE III

Measurements of Manus and Pes
(All measurements in mm)

		R5830 L	R5830 R	R2466 L	SM4127 R	R196 L	R196 R	R200	Manus R196 R
First metatarsal	L	–	–	–	–	–	46	± 56	13
	Wp	–	–	–	–	–	10	12	8
	Wd	7	7	6	14	12	13	15	6
Phalanx	I	18·5	–	–	–	28	29	–	8
	ungual	–	–	± 15	–	23	–	–	+ 8
Second metatarsal	L	55	54	± 65	69	–	66	± 83	21
	Wp	–	8	–	8	–	12	–	11
	Wd	9	9	–	13	–	15	19	11
Phalanx	I	–	–	25	–	29	28	–	12
	II	–	–	± 19	–	21	–	–	8·5
	ungual	–	–	22	–	–	–	–	–
Third metatarsal	L	62·5	63	± 70	77	–	84	106	24
	Wp	8	7·5	–	9	–	10	15	9·5
	Wd	11·5	–	14	15	–	18	22	8·5

Table III (*cont.*)

		R5830 L	R5830 R	R2466 L	SM4127 R	R196 L	R196 R	R200	Manus R196 R
Phalanx	I	–	–	25	–	28	25	–	10
	II	–	–	19	–	23	21	–	7
	III	–	–	16	–	–	–	–	5
	ungual	–	–	± 23	–	–	–	–	app. 8
Fourth metatarsal	L	55·5	53	± 59	72	–	69	± 90	15
	Wp	9	9	–	13	–	15	–	7
	Wd	9·5	9	± 10	14	–	14	20	6
Phalanx	I	–	–	± 17	–	19	18	–	5
	II	–	–	15	–	15	17	–	3·5
	III	–	–	13	–	14	–	–	–
	IV	–	–	12	–	12	12	–	?
	ungual	–	–	17	–	–	–	–	–
Fifth metatarsal	L	–	–	–	23	–	24	35	10
	Wp	–	–	–	6	–	9	8	6·5
	Wd	–	–	–	3	–	–	5	5

III. THE *HYPSILOPHODON* BED

a) *Stratigraphy*

Casey (1963) showed that the onset of the Cretaceous period in Southern England is indicated by the marine invasion that formed the Cinder Bed at the base of the Durlston Beds in the Middle Purbeck Series. The rest of the Durlston Beds and the succeeding Wealden Series consist mainly of lagoon and deltaic deposits. The Lower Greensand, Gault and Upper Greensand beds are marine and represent the remainder of the Lower Cretaceous in this region (B.M. (N.H.) Handbook 1962, Hughes 1958), although Kirkaldy (1939, 1963) has included the last two in the Upper Cretaceous with the Chalk. On the Isle of Wight there is no exposure of the equivalents of the Hastings Beds of the Weald but only of the younger beds of the Weald Clay, here represented by the Weald Marls with the overlying Shales. Remains of *Hypsilophodon*, which occur next to the contact between the Marls and the Shales, have been found only in Brightstone (= Brixton) Bay, although this contact is also exposed in the cliffs of Compton Bay and Sandown Bay (White 1921). The absence of ostracods in the Marls and the lower part of the Shales makes it difficult to determine accurately the age of the *Hypsilophodon* Bed. It is probably Barremian (Allen 1955, B.M. (N.H.) Handbook 1962, Hughes 1958) but it might possibly be Early Aptian (Hughes 1958) (see Text-fig 64).

The *Hypsilophodon* Bed is exposed in the cliff at beach level about 100 yd west of Cowleaze Chine and rises in the cliff to end about $\frac{3}{4}$ mile further west just beyond Barnes High (White 1921, fig. 1b, c; Chatwin 1960, fig. 17b, c). A detailed succession of these marls and shales was given by Strahan (1889) who gave two descending sections of the beds at the junction region. He noted that the first (page 13), between Cowleaze and Barnes Chine, was taken from various points in the cliffs :

'. . .

Grey and black shales, the upper part interlaminated with much sand in Cowleaze Chine ; a band crowded with *Paludina* and *Unio* near the top, and another with *Cyrena* and *Paludina* near the bottom	19′ 0″
White sand and clay, with lignite	2′ 6″
Current-bedded white rock	2′ 6″
Reddish-blue sand and clay, with bone fragments (*Hypsilophodon* Bed)	3′ 0″
Red and variegated marls	44′ 0″

. . .'

while the second (pages 14–16), from Atherfield to near Brook, gave the succession at Cowleaze Chine :

'. . . about 144′ . . .

Wealden shales	Blue shales, with *Unio* and *Paludina* in the top, and *Cyrena* and *Paludina* near the bottom	19′ 0″
	White sand and clay	2′ 6″
	White rock	2′ 6″
	Red sand, with bones (*Hypsilophodon* Bed)	3′ 0″
Wealden marls	Red and mottled marls, rocky and ripple-marked at the top	44′ 0″

. . . about 510′ . . .'

Judging on the lithology of these localities today, Strahan interchanged the two sections – it will be noted that 'sand in Cowleaze Chine' is mentioned in the section which purports to relate to the cliff-section rather than to the beds at Cowleaze Chine.

White (1921 : 16) noted that near Cowleaze Chine the white rock 'is a pale, calcareous, silty stone, indistinctly shaly in places, and having an uneven base [see Galton 1967, fig. 3A]. It contains *Unio* and water-worn bones'. The articulated material found by Dr P. L. Robinson was in this shaly portion as well as in the *Hypsilophodon* Bed below. Hooley, as noted by White (1921), found remains of *Hypsilophodon* in the Marls a little below the *Hypsilophodon* Bed but not in the Shales above.

White (1921 : 16) reproduced the second succession of Strahan (1889) and noted that the *Hypsilophodon* Bed, although included with the shales, 'is lithologically and stratigraphically more nearly allied to the marls'. As noted by Hulke (1882), the *Hypsilophodon* Bed is extremely variable, even within the space of a few yards. This is certainly true of the first hundred metres exposed in the cliff near Cowleaze Chine. Here the bed consists of reddish-blue marls which are indistinguishable from the Marls below. In the lower part of the Bed there are, in addition, several rocky bands of varying thickness which also occur near the top of the Marls (see Galton 1967, figs. 3B, C). About 160 m west of Cowleaze Chine there are well-developed desiccation cracks in the marls (see Galton 1967, fig. 3C). These cracks, which are about 45 cm deep and 4 cm wide, are filled with sand continuous with that of the overlying rocky band. It is difficult to determine whether this band is at the top of the Marls or at the base of the *Hypsilophodon* Bed.

b) *Hypsilophodon* localities

Lydekker (1888) listed specimens of *Hypsilophodon* and in each instance the locality, where given, was Cowleaze Chine. Swinton (1936*b* : 213) stated that 'almost every specimen comes from Cowleaze Chine' while, in connection with the two skeletons from the Hooley Collection, he stated (1936 : 555) that 'these two specimens, like the type, are from the Wealden of Cowleaze Chine'. The *Hypsilophodon* Bed where it crosses the mouth of Cowleaze Chine is buried underneath 12 ft of shingle. If all the specimens actually came from the Chine then this productive site is now very rarely accessible.

Owen (1855 : 2) stated that 28707 'was discovered . . . about one hundred yards west of Cowleaze Chine . . . the mass of Wealden stone . . . was broken into two parts in its extraction from the bed'. Owen (1874 : 12, 13) quoted from a letter written by Fox in 1870 as follows (specimen numbers have been added) : 'This jaw [R189] was found within a yard of the skull [R197 – the holotype]. They were both in a mass of mud that had slided down from the cliff . . .', and '. . . you will find one very small tooth [R191], quite perfect, that came out of this slab [R190] in dressing. This slab [R190] was found in the fallen cliff, about 150 yards east of Barnes High. . . . The skull [R197 – holotype] and broken jaw [R189] were found about 60 yards further eastward.' All these specimens were listed by Lydekker (1888) as from Cowleaze Chine, whereas the actual site is at the opposite end of the bed, a little over half a mile further west. Consequently the entry 'Cowleaze Chine' is equivalent to *Hypsilophodon* Bed ; this is all the data we have for specimens R192–R196 and R200 (Fox MS).

Hulke (MS) gave nearly all his localities as near Cowleaze Chine and exact details were given only for R2466–R2476 which was found about 100 yd west of the Chine (not the west end of the bed as stated by Hulke, 1874 : 18). In a memorandum dated Oct. 1894, Hulke (MS, opposite find no. 260) wrote that 'I do not suppose the Cowleaze end of this bed richer than the other parts of it, but its waste is greater and fresh exposures are frequent'. The locality for R5829 and R5830 was near Cowleaze Chine and the two recent finds of *Hypsilophodon* were both about 100 m west of the Chine. Consequently more material may be found in the productive region about 100 m west of the Chine.

c) *Fauna*

The Wealden of the Isle of Wight is famous for its dinosaurs but most of these are represented by very fragmentary remains (for details see Swinton 1936*b*). Apart from the *Hypsilophodon* material, only two other reasonably complete skeletons have been found – those of *Iguanodon atherfieldensis* and *Polacanthus foxii*. Both represent large animals (about 5 m) whose cadavers were probably carried some distance by water. The fragmentary and broken nature of the other dinosaurian remains indicates that they were transported quite a long distance.

In marked contrast to this is the *Hypsilophodon* Bed, from which well preserved and naturally articulated bones representing 20 individuals of this relatively small dinosaur have been found. Three of these (R196, R5829, R5830) are reasonably complete skeletons. The incomplete nature of the remainder reflects faults of discovery rather than of preservation because, in most instances, the edges of the blocks cut across articulated bones. The skeleton of R196 is almost complete and nearly all the bones were in natural articulation. It is unlikely that this individual was carried very far, if at all, from where it died. The same is true of the two skulls of young individuals (R197, R2477) in which the fragile bones are excellently preserved and only slightly disarticulated. In a few instances (R196, R2477, U.C.L.) two or three skeletons have been preserved very close to each other in the same small block.

The 'fauna' represented in the *Hypsilophodon* Bed is very restricted. Apart from *Hypsilophodon*, Hulke (1882 : 1036) recorded the presence of 'a small scuted crocodile (*Goniopholis*?) and a chelonian (*Trionyx*?)'. He also noted that neither Fox nor he had found any remains of *Iguanodon mantelli* in this bed. In the Hooley collection there is a cervical vertebra that is probably *Goniopholis* and a phalanx that might be from *Iguanodon*, but it is not certain that these came from the *Hypsilophodon* Bed. The same is true of the proximal end of a small femur, possibly of *Iguanodon*, which is catalogued with several odd femora of *Hypsilophodon* (R170). The coelurosaur *Calamospondylus foxi* may not have come from the *Hypsilophodon* Bed, because the tibia is not listed as such by Fox (MS). Why *Hypsilophodon*, which is represented by such excellent material, is the only dinosaur found in the Bed is a mystery. This, however, is certainly the case, because Fox, Hulke and Hooley collected much material from this Bed (full list in Galton 1967), all referable to *Hypsilophodon*.

IV. OSTEOLOGY OF *HYPSILOPHODON FOXII*

Order ORNITHISCHIA

Suborder ORNITHOPODA

Family **HYPSILOPHODONTIDAE** Dollo 1882 (page 175)

Genus ***HYPSILOPHODON*** Huxley 1869 (page 3)

EMENDED DIAGNOSIS. Five premaxillary teeth separated by step from maxillary row with 10 or 11 teeth, 13 or 14 on dentary ; enamelled medial surface of a dentary tooth has a strong central ridge that is absent on the lateral surface of a maxillary tooth. Narial openings completely separated by anterior process of premaxillae ; large antorbital recess or depression plus row of large foramina in maxilla ; jugal does not contact quadrate ; large fenestrated quadratojugal borders lower temporal opening. Five or six sacral ribs, the additional one borne on the anterior part of the first sacral vertebra. Scapula same length as humerus ; obturator process on middle of ischium. Femur with following combination of characters: fourth trochanter on proximal half, lesser trochanter triangular in cross-section with a shallow cleft separating it from the greater trochanter, practically no anterior condylar groove and posteriorly outer condyle almost as large as inner. The type-species, *H. foxii*, is the only species known.

HOLOTYPE. British Museum (Natural History) No. R197.

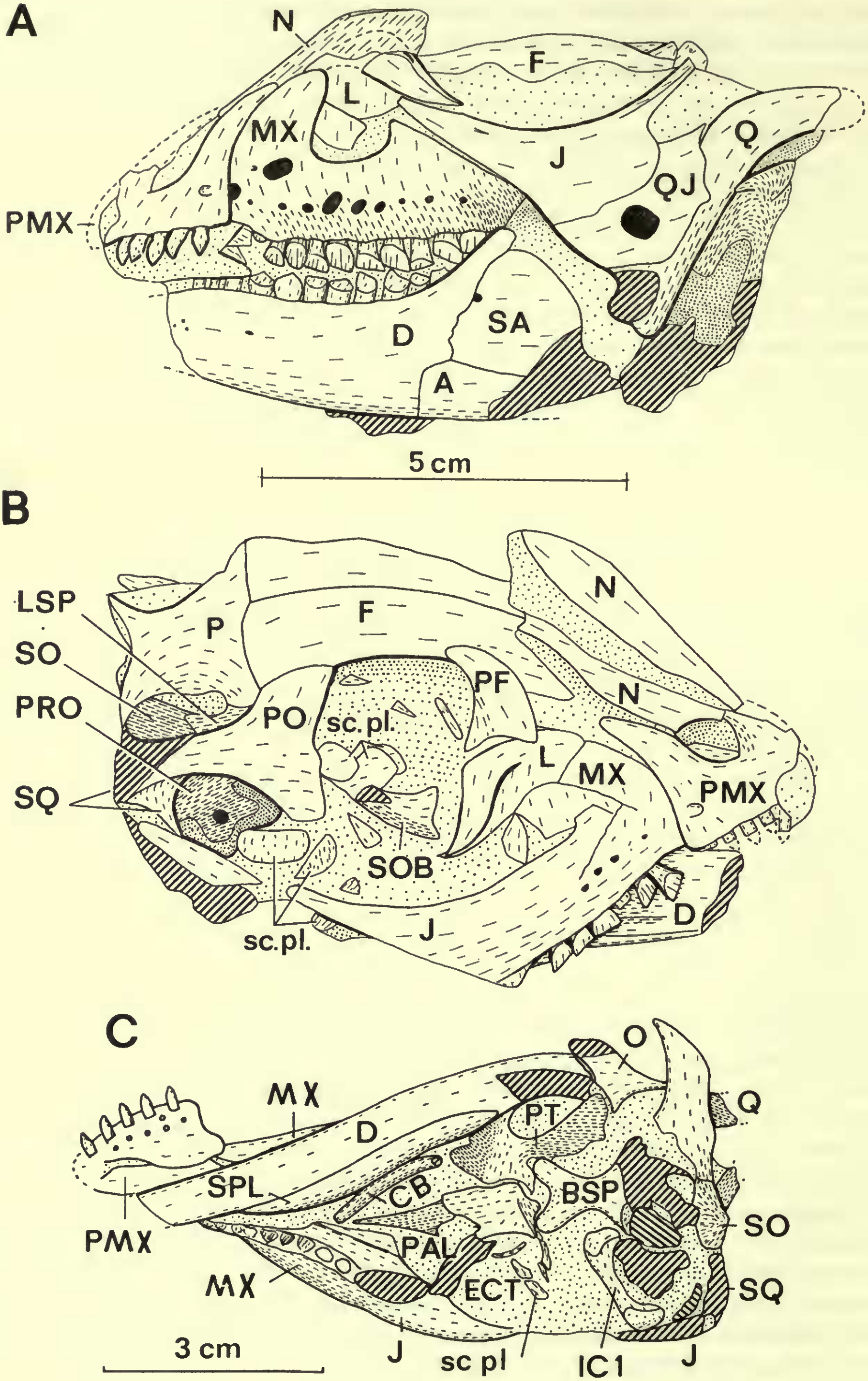
PARATYPE. British Museum (Natural History) No. 28707.

Huxley read his paper on *Hypsilophodon* on 10 November 1869; this was published in 1870 and citations are given as *Hypsilophodon* Huxley 1870. However, later authors have overlooked a summary of this paper published in 1869; the year of publication is confirmed by a reference in abstract in the *Proceedings of the Geological Society* No. **205** p. 4 to the papers which were to be given at the next meeting on 24 November 1869. This summary provides an adequate diagnosis of *Hypsilophodon foxii* which is certainly more detailed than that given by Boulenger (1881) for *Iguanodon bernissartensis*.

Specimens used for osteology and reconstructions

The individual skull bones of R2477 were stuck together with Carbowax (polyethylene glycol 4000) and their spatial relationships are maintained in all the figures of this specimen. The description of the skull is mostly based on this specimen as is the reconstruction of the complete skull (Text-fig. 3). Certain details are from other specimens: the anterior end of the premaxilla is from R196, the premaxillary teeth and the quadratojugal are from R197, the supraorbital is from R194 and R197 and the predentary is from R2470. The mandibular ramus is based on R196 with supplementary details from specimen R192, R197, R2470, R2477 and R8418. The restored lengths of the dentary and of its tooth row are probably not absolutely accurate because the jaw is reconstructed from several incomplete specimens of different size. The size of the predentary is approximate because the only specimen is of a small individual. The spatial relationship between the articular head of the quadrate and the end of the tooth row is accurate as this is based on the lower jaw of R2477. The jugal is adapted from R197 and R2477 but the resulting quadratojugal (Text-fig. 3) is proportionally rather longer ventrally than that of R197 (Text-fig. 2). In the reconstruction the basipterygoid processes are separated by about 7 mm from their original contact with the pterygoid. This indicates that the braincase should be situated some 7 mm more anteroventrally. However, if the parietal, squamosal and quadrate are also moved by the same amount the posterior teeth of the lower jaw fail to engage the corresponding teeth of the maxilla.

The reconstruction of the postcranial skeleton (Text-fig. 62) and the osteology of the individual elements (apart from the femur, tibia and fibula, for which R5830 is used) are based on the nearly complete skeleton of R196 and the tail R196a. Individual variations exhibited by specimens other than R2477, R196 and R5830 are noted after the description of the element concerned. In the Text-figures all bones are drawn from the left side unless otherwise stated.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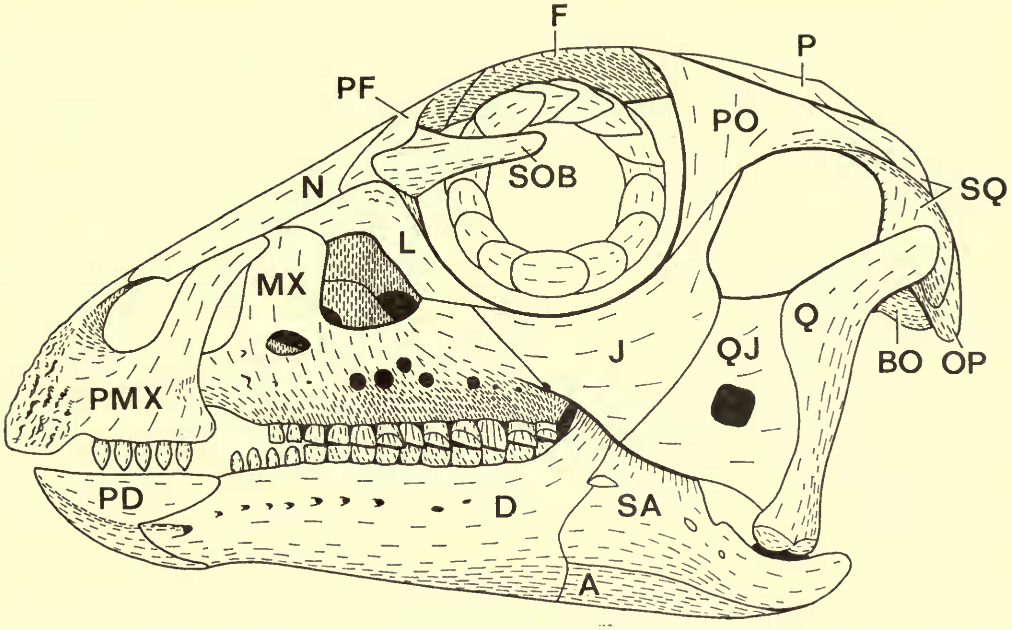


FIG. 3. *Hypsilophodon foxii.* Skull reconstruction, mainly R2477 × 1. For abbreviations see below; for specimens used see page 19.

a) *The skull and lower jaw*

i) INDIVIDUAL BONES

Supraoccipital (SO). This bone forms the dorsal boundary of the foramen magnum. The posterior surface (Text-fig. 8) which is inclined forwards at an angle of about 55 degrees to the skull axis (Text-fig. 5A), is flat ventrally but bears a median ridge dorsally. The surface on either side of this ridge is concave and sweeps obliquely outwards, forming a dorso-lateral corner with the lateral part of the bone. This forms part of the side-wall of the braincase and is concave antero-posteriorly and to a lesser extent dorso-ventrally (Text-fig. 5C). Apart from the median ridge the dorsal and medial parts of the bone are quite thin. The ventro-lateral part, especially more posteriorly, is very thick. The ventral surface is gently convex antero-posteriorly but strongly concave transversely.

FIG. 2. *Hypsilophodon foxii.* Holotype, R197. Skull × 1. A, left side; B, right side; C, ventral view. Abbreviations used in Text-figs. 2–16

A	angular	F	frontal	PSP	parasphenoid	QJ	quadratojugal
ART	articular	J	jugal	PA	prearticular	sc.pl.	sclerotic plate
BO	basioccipital	L	lachrymal	PD	predentary	SPL	splenial
BSP	basisphenoid	LSP	laterosphenoid	PF	prefrontal	SQ	squamosal
CB	ceratobranchial	MX	maxilla	PMX	premaxilla	SO	supraoccipital
CO	coronoid	N	nasal	PO	postorbital	SOB	supraorbital
D	dentary	OP	opisthotic	PRO	prootic	SA	surangular
ECT	ectopterygoid	P	parietal	PT	pterygoid	V	vomer
EO	exoccipital	PAL	palatine	Q	quadrate		

The end part of the dorso-lateral corner has suture markings (Text-fig. 5C, Pl. 2, fig. 1) while anteriorly there is a lateral groove that becomes wider as it runs diagonally across the side-wall. From the central part of this groove a ventral groove arises that passes through the floor of the lateral groove. The vena capitis dorsalis probably ran in the anterior part of the lateral groove and then into the ventral groove. Anteriorly it was bounded laterally by the parietal that enclosed the dorsal part of the supraoccipital (Text-fig. 5A) and fitted against the side-wall adjacent to the groove. In passing ventrally the vena capitis dorsalis passed medially to the edge of the parietal. More posteriorly the edge of the parietal fitted into the tapering posterior part of the lateral groove and on to the sutural surface of the dorso-lateral corner. The opisthotic is sutured to the obliquely truncated postero-lateral corner of the supraoccipital which has a large and almost square sutural surface. The prootic is sutured to a triangular surface on the ventral edge and, like the surface for the opisthotic (both visible in R8418), it has well-developed sutural ridges. The sutural junction with the prootic is excavated medially to form a large tapering tunnel, the fossa subarcuata (Text-fig. 9B, C), which was probably for the floccular lobe.

Exoccipital (EO). The suture between the exoccipital and the opisthotic is not visible in R2477. In R8418 on the medial surface there is a sutural line (Text-fig. 9B) but unfortunately this cannot be followed on to the other surfaces. The exoccipital forms the ventro-lateral border of the foramen magnum while the round posterior surface forms part of the occipital condyle. The ventral surface has strong sutural ridges for the basioccipital.

Basioccipital (BO). This forms most of the sub-spherical occipital condyle whose smooth articular surface is well developed ventrally (Text-fig. 6A) as well as posteriorly (Text-fig. 8). Anteriorly from the condyle there is a tapering median ventral ridge (Text-fig. 6A) with well-developed insertion markings. In R5830 the anterior surface, which is more or less vertical, has two subcircular areas for the buttress of the basisphenoid. On each side there are two obliquely inclined lateral surfaces, with well-developed sutural ridges, which are set at an angle of about 135 degrees to each other. The smaller anterior surface is for the basisphenoid while the larger surface is for the opisthotic and also, more posteriorly, for the exoccipital.

Opisthotic (OP). This forms the lateral wall of the foramen magnum (Text-figs. 4B, 9A). The paroccipital processes of R2477 are missing but have been restored with reference to specimens R194 and R196. The proximal end of the bone is thick, roughly triangular in cross-section, with a ventrally directed part that continues the side-wall of the braincase (Text-fig. 9A). The bone tapers laterally, with the anterior edge gradually disappearing, to form a flattened paroccipital process (Text-fig. 9A). The anterior edge is flat, forming a sutural surface for the prootic. Dorsal to this the surface of the proximal half is laterally concave as it is ventrally where this curve is much more strongly developed. The ventral edge is thick and rounded proximally but becomes thinner laterally. The dorsal edge is thin and moderately sharp along all its length.

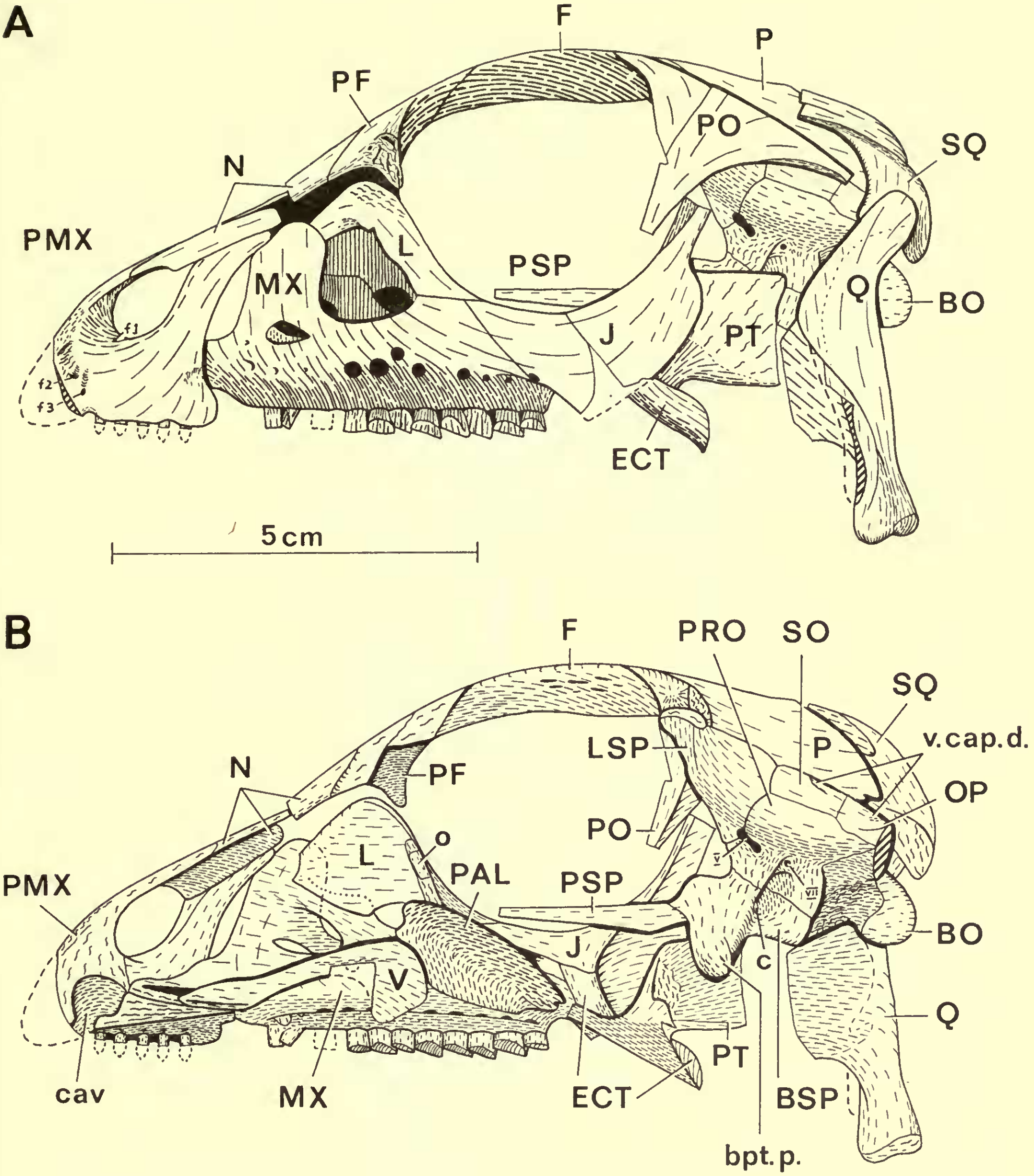
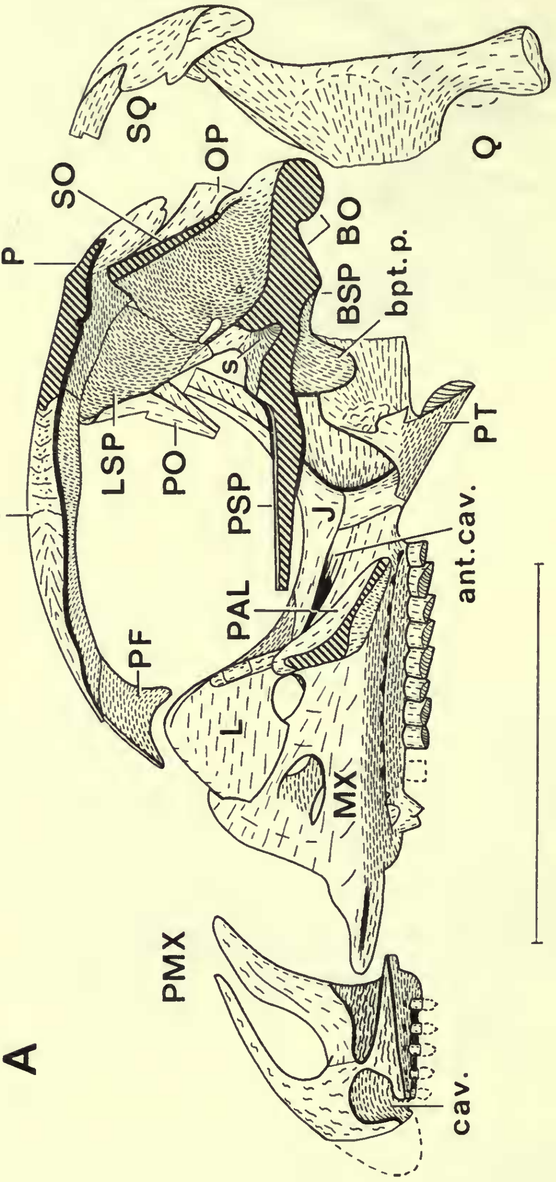


Fig. 4. *Hypsilophodon foxii.* Skull R2477 × 1. A, lateral view, compare with Pl 1, figs. 3, 4; B, medial view, as A but with lateral bones of the left side removed, compare with Pl. 2, fig. 2. Abbreviations: bpt p., basipterygoid process; c, foramen for internal carotid artery; cav, cavity in the premaxilla; o, bony element; v. cap. d., vena capitis dorsalis; V, trigeminal foramen; VII, facial foramen. For other abbreviations see page 21.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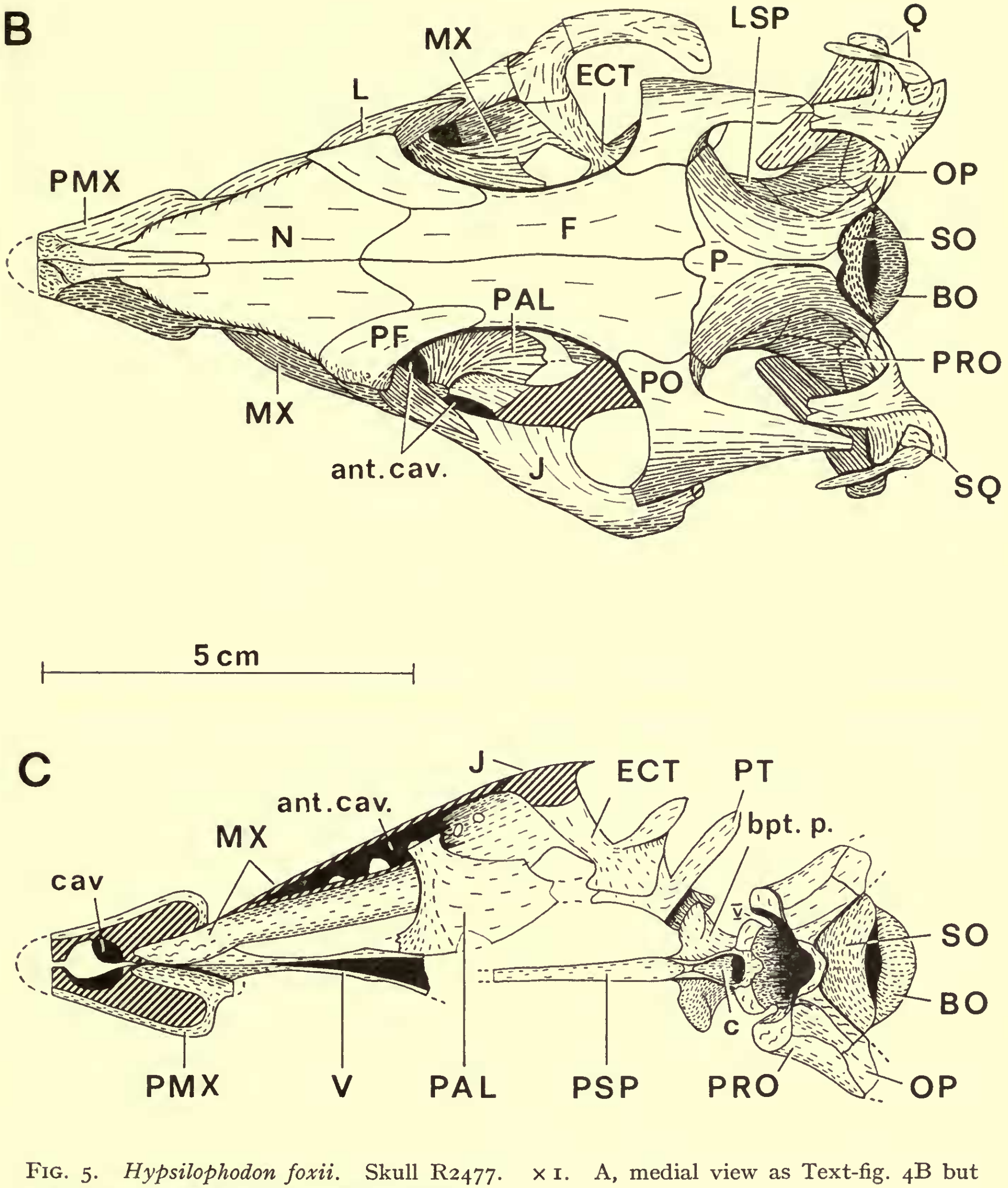


Fig. 5. *Hypsilophodon foxii.* Skull R2477. × 1. A, medial view as Text-fig. 4B but with braincase and palatine sectioned, nasals and vomer removed, premaxilla, squamosal and quadrate displaced ; B, dorsal view, compare with Pl. 1, fig. 1 ; C, dorsal view of the palate and braincase, as B but with bones of the skull roof and most of the left side removed, premaxillae, maxilla and jugal sectioned, compare with Pl. 2, fig. 1. Abbreviations : ant. cav., antorbital cavity or fossa ; bpt.p., basipterygoid process ; cav., cavity in premaxilla ; s, sella turcica ; V, trigeminal foramen. For other abbreviations see page 21.

The ventral surface of the braincase side-wall forms a rectangular surface with well-developed sutural ridges (visible in R8418) for the basioccipital. The anterior part of this wall forms an irregularly shaped sutural surface with well-developed sutural ridges for the prootic. The fenestra ovalis, middle ear cavity, internal auditory meatus and the jugular foramen are situated between the opisthotic and the prootic (Text-fig. 9). The tapering postero-dorsal part of the prootic also sutures to the flat-topped anterior edge of the opisthotic. The surface for the supraoccipital (Text-fig. 9B) has strong sutural ridges. The adjacent dorsal edge contacted the squamosal which is overlapped by the paroccipital process (Text-fig. 8).

Prootic (PRO). This is an irregularly shaped bone (Text-fig. 9) which forms part of the lateral wall of the braincase. The dorsal part of the bone continues the dorso-ventrally convex curve from the adjacent laterosphenoid (Text-fig. 4B). This curve becomes more acute passing posteriorly where the prootic tapers to a point which overlaps the paroccipital process (Text-fig. 9A). The ventral part is concave dorso-ventrally but this curve is complicated by three foramina (Text-fig. 9A). Posterior and ventral to the foramen ovale (V) the surface slopes gently away from the foramen but dorsally the slope is steeper, as it is around the facial foramen (VII), while the posterior edge is vertical. The sides of VII spiral slightly so that the steeper anterior surface forms a step above the ventral edge. This step is continued antero-ventrally where it becomes more pronounced as there is a well-developed depression at this point. Dorsally the depression is overhung by a thin and sharp edge. The prootic is sutured to the laterosphenoid, supraoccipital, opisthotic and basioccipital.

Basisphenoid (BSP). This median bone forms a thick floor to the anterior part of the braincase (Text-fig. 5A). In ventral view (Text-fig. 6A) the posterior part forms two buttresses which abut against the basioccipital and slightly overlap this vertical suture. The two buttresses, which are separated by a median depression, taper anteriorly with the lateral edges becoming thinner and sharper. The diverging pterygoid processes have, on the anterior part of their base, a well-developed depression which is continued on to the base of the parasphenoid. Adjacent to this depression the anterior edge is thin and sharp but more distally it is much thicker and rounded.

In lateral view (Text-fig. 4B) the distal part of the basipterygoid process has a rough surface which, with its continuation on to the rounded anterior edge and a smaller but similar surface on the medial surface, articulated with the pterygoid. The posterior edge of the process is thick and rounded and it continues postero-dorsally across the side of the basisphenoid. There is a deep excavation of the side of the bone postero-ventral to this edge so that there is only a thin median sheet. This thickens considerably postero-laterally and the excavation becomes progressively shallower. The ventral edge is formed by the buttress which is latero-ventrally flattened. The excavation and its bordering diagonal edge are continued on to the adjacent surface of the prootic. Anterior to this diagonal edge the surface of the basisphenoid is rough textured. The dorso-median part of the bone is deeply excavated to form the pituitary fossa (Text-figs. 5A, C) from which paired foramina for the carotid arteries pass postero-laterally, one on each side of the thin median sheet (Text-fig. 6A).

Parasphenoid (PSP). This arises from the basal region of the basipterygoid processes, anterior to the pituitary fossa, and runs forward to bisect the posterior part of the palatal vacuity (Text-fig. 6A). This tapering process is triangular in cross-section, with a concave dorsal surface, and the edges are thin and sharp. Its anterior limit cannot be determined in R2477.

Laterosphenoid (LSP). The lateral surface (Text-fig. 4B) is gently concave antero-posteriorly and convex dorso-ventrally ; there is a well-developed depression on the ventral part running antero-dorsally from the foramen ovale (V). The dorsal end of the bone is expanded laterally (Text-fig. 7B) to form a head, the rounded dorsal surface of which fits into a cavity formed by the frontal and postorbital (Text-fig. 6B). The anterior surface is flat and tapers ventrally (Text-fig. 7B). The medial surface (Text-fig. 5A) is dorso-ventrally concave while antero-posteriorly it consists of two very gently concave areas separated by a very gently convex ridge.

The dorsal surface for the parietal is thin and flat with a few minor ridges. The thin dorsal part of the posterior edge is gently rounded for the supraoccipital. More ventrally this edge is much thicker and formed the sutural surface for the prootic. The suture is obliquely inclined with the laterosphenoid overlapping the prootic (Text-figs. 9A, C). Just above the foramen ovale (Text-fig. 9A) there is a notch in the margin to receive a process of the prootic. Ventrally the second surface for the prootic is vertical, flat and triangular in outline.

Orbitosphenoid. This is not represented by the ossified plate present in *Parksosaurus* (see Galton, in press) and *Camptosaurus* (see Gilmore 1909). Anteriorly on the medial part of the laterosphenoid head there is a slight step, continuous with the straight antero-medial edge (Text-figs. 6B, 7B), while on the adjacent edge of the frontal there is a groove (Text-fig. 6B). These probably represent two of the contact surfaces of the orbitosphenoid which may not have been ossified.

Premaxilla (PMX). Each premaxilla has an anterior and a posterior process (Text-fig. 4A) while medially there is a ventral sheet (Text-fig. 6A). The narial opening is bordered by the anterior process which, together with its fellow on the other side, wedges between the nasals (Text-figs. 5B, 6B) so that they overlap very slightly. This process, triangular in cross-section, has a lateral edge which continues on to the main body of the bone (Text-fig. 4A). The surface in front of this edge is covered with large knobs while more ventrally there are two foramina (f_2, f_3, Text-fig. 4A). The rough and knobbly anterior end of the premaxilla was probably covered by horn to form a beak. Behind this edge the surface is concave and it is more obliquely inclined on the process, at the base of which there is another foramen (f_1). The posterior half of the lateral surface is gently convex antero-posteriorly (Text-fig. 5B) and concave dorso-ventrally (Text-fig. 7A). Anteriorly the posterior process is gently rounded while posteriorly the edge is thin and sharp. More ventrally the bone is thicker with a well rounded edge (Text-fig. 7A).

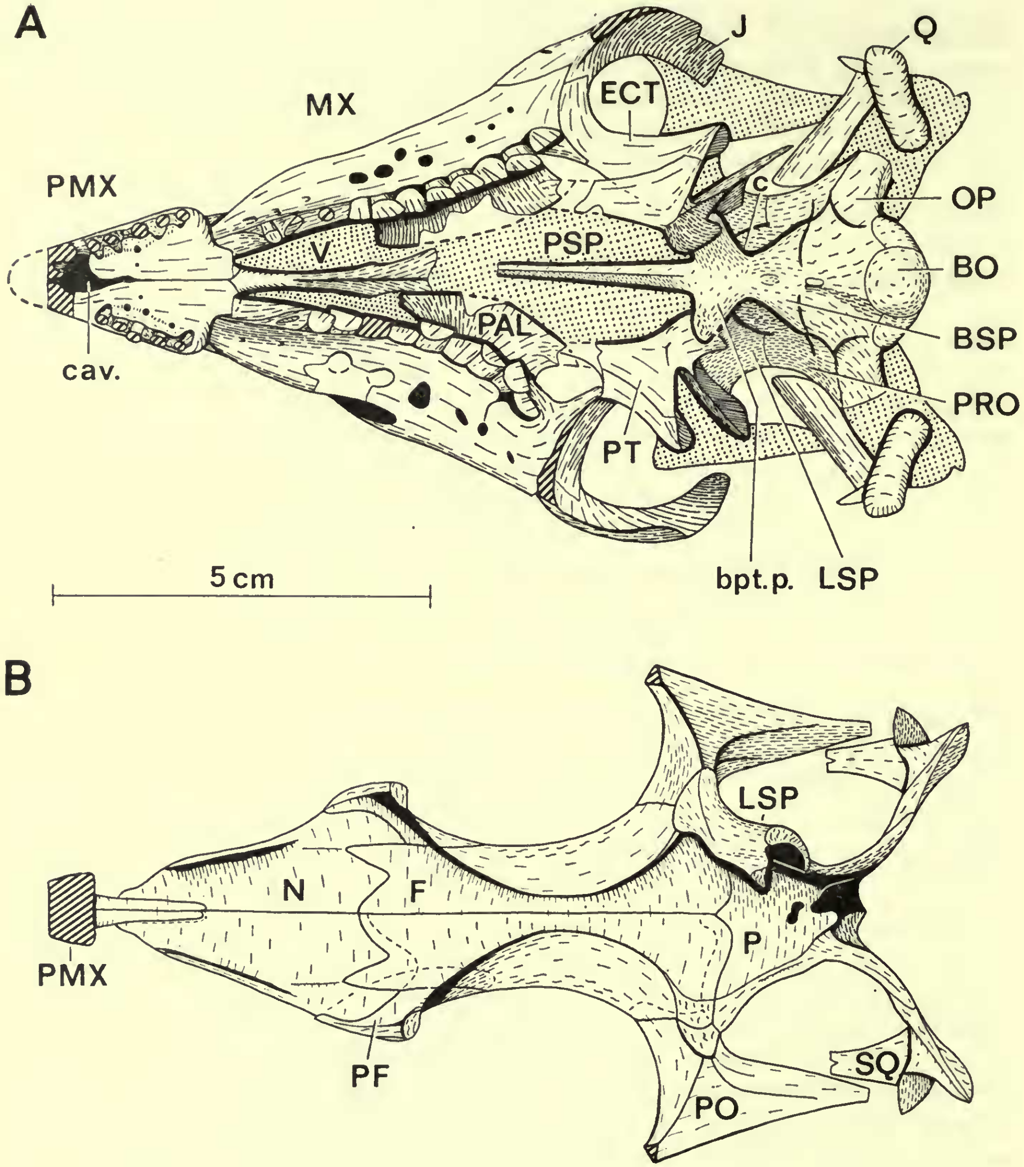


FIG. 6. *Hypsilophodon foxii*. Skull R2477, ×1. A, palatal view, compare with Pl. 1, fig. 2; B, ventral view of the skull roof. Abbreviations: c, foramen for internal carotid artery; cav., cavity in the premaxillae; bpt. p., basipterygoid process. For other abbreviations see page 21.

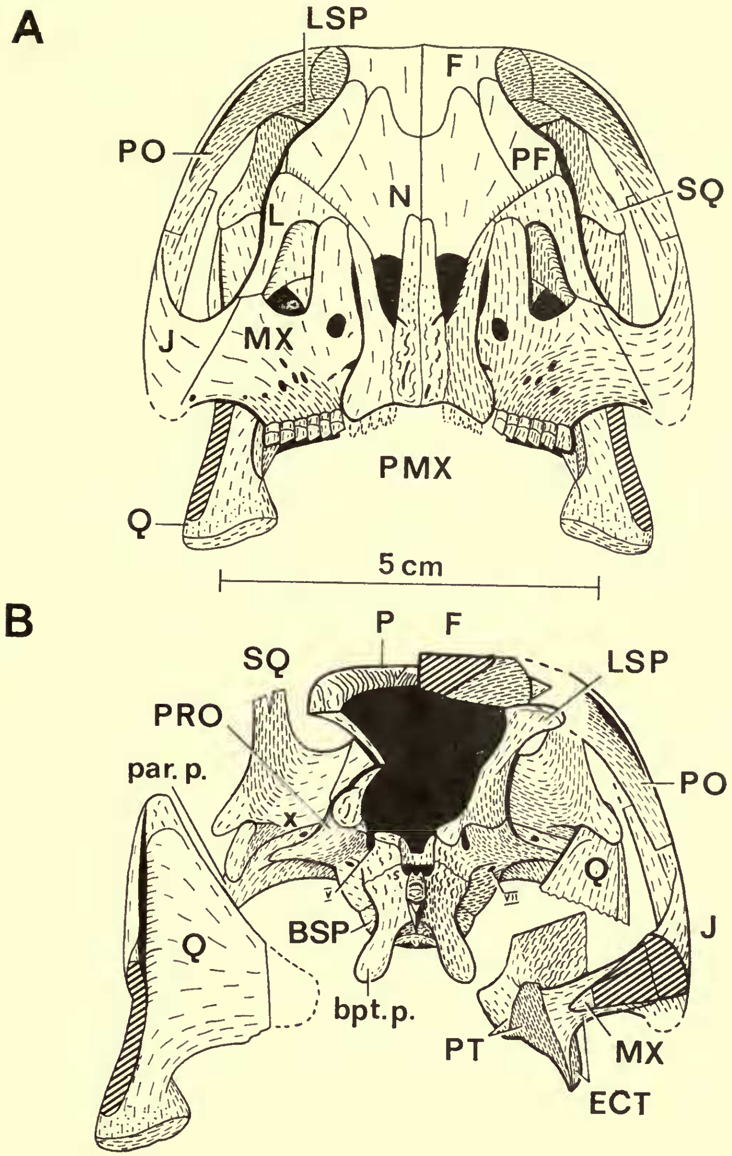


FIG. 7. *Hypsilophodon foxii.* Skull R2477, × 1. A, anterior view; B, anterior view with skull sectioned through the middle of the orbits with the frontal, orbital and palatal bones of the right side removed and the quadrate displaced. Paroccipital process restored from R194. Abbreviations: bpt. p., basipterygoid process; par. p., paroccipital process; s, sella turcica; x, remnant of post-temporal fenestra; V, trigeminal foramen; VII, facial foramen. For other abbreviations see page 21.

The ventral surface (Text-fig. 6A) is transversely concave with five marginal thecodont teeth, each with a foramen medial to it. In R5830 and R8367 the median surface of the tapering ventral sheet and of the anterior process form one continuous flat sutural surface for the other premaxilla. In R197 and R2477 (Text-fig. 4B) these two surfaces are separated by a large depression which communicates with the exterior ventrally (Text-fig. 6A). Above the tapering ventral sheet there is a large channel which tapers in the opposite direction (Text-fig. 5A) with longitudinal ridges. This channel receives the anterior process of the maxilla and also the median vomer more postero-ventrally (Text-figs. 4B, 5C). Above this channel the surface is slightly concave. In R2477 the dorsal part of the posterior process sutures medially with a flange on the nasal (Text-figs. 4A, B). The sutural union is delimited by a slight edge which then curves antero-ventrally. In R197 the posterior process contacts the maxilla all along its posterior border (Text-fig. 2A).

Maxilla (MX). The maxilla consists of a thick rod with ten or eleven tooth-sockets (Swinton 1936, fig. 1). On the medial surface (Text-fig. 5A) there is a longitudinal ridge, convex transversely, which is continued anteriorly as a process. This process, triangular in cross-section, is slightly off-set from the rest of the ridge (Text-fig. 5C) and it bears strong sutural ridges. The two maxillary processes and that of the vomer fit tightly into a cavity enclosed by the premaxillae (Text-figs. 4B, 5A, C). The limit of overlap on the lateral surface is indicated by an edge that is a continuation of the sharp edge at the anterior end of the tooth row.

Above the main tooth-bearing region the maxilla consists of two thin fenestrated sheets which enclose the antorbital fossa (Text-figs. 4, 5, 60B, C). The lateral sheet arises from the side of the main body that it overhangs (Text-fig. 6A). This sheet has several foramina of varying size (Text-fig. 4A) while, more dorsally, it forms the anterior and ventral margins of the antorbital fenestra. The medial sheet forms a thin dorsal edge to the main body immediately above the roots of the teeth. This sheet has a much shallower vertical curve than the lateral sheet that it joins in the middle of the antero-dorsal part (in front of the antorbital fenestra, Text-fig. 5A). The more dorsal part of the medial sheet is overlapped by the thin sheet of the lachrymal (Text-fig. 5A) with which it forms the medial wall of the antorbital fenestra (Text-fig. 4A) and fossa. There is a large fenestra anteriorly in the medial sheet of the maxilla, while posteriorly, where it tapers to nothing, it borders another large fenestra with the lachrymal (Text-fig. 5A). The posterior margin of the latter is formed partly by the palatine bar and possibly also by the maxilla below. Posterior to this bar the antorbital fossa opens dorsally and posteriorly (Text-fig. 5) with the sides, especially medially, becoming progressively shallower (Text-fig. 5A). The medial wall of this part is formed by the main body of the maxilla with the thin lateral sheet curving dorso-laterally. The jugal forms an inwardly projecting ledge which roofs the more lateral parts of the fossa (Text-figs. 5B, C). The posterior end of the maxilla is sharp-edged and straight, making an angle of about 45 degrees with the vertical.

In R2477 the lateral sheet contacts the premaxilla only dorsally (Text-fig. 4A) and there is a narrow vacuity. The lateral sheet is extremely thin yet it has a perfect edge and it is the same on both sides. Consequently the thin anterior edge was not completely ossified in R2477 ; this, however, must be an individual variation because in R197 the lateral sheet is proportionately larger with an extra foramen and is completely overlapped by the premaxilla (Text-fig. 2). The lachrymal overlaps the medial surface of the medial sheet while posteriorly it contacts the thin edge of the lateral sheet in R2477 (Text-fig. 4A), though not in R197 (Text-fig. 2A). Ventral to the bridging bar of the palatine there is part of the medial sheet of the maxilla which probably also touched the lachrymal. The main body of the palatine is sutured diagonally on to the medial surface of the maxilla (Text-figs. 4B, 5A, C) with fine parallel suture ridges postero-ventrally but the surface is more irregular antero-posteriorly near the bar. The lateral sheet of the maxilla forms an overlapping suture with the jugal in R2477 (Text-fig. 4A) but in R197 (Text-fig. 2A) only the edge fits against the jugal more anteriorly. The jugal also sutures to the lateral part of the wedge-shaped posterior end of the maxilla which, with the medially directed process it bears (Text-fig. 5B), fits into a groove in the ectopterygoid.

Nasal (N). The nasals are rather thin and one slightly overlaps the other. The lateral margin of the nasal is turned downwards anteriorly to form a vertical sheet, the lower part of which is overlapped by the posterior process of the premaxilla. The tapering posterior part of the nasal overlaps the frontal while more laterally it is overlapped to a progressively greater extent by the prefrontal (Text-figs. 5B, 6B). This is greatest near the lateral edge where the prefrontal fits into a groove in the side of the nasal. This groove continues on to the latero-ventral edge of the nasal where it receives the lachrymal.

Parietal (P). In dorsal view (Text-fig. 5B) the anterior part of the single parietal is flat but the sides are obliquely concave and transversely constricted with a thin median edge. In anterior or posterior view (Text-fig. 8) there are two postero-lateral wings which are twisted along their long axis ; the axis is somewhat obliquely inclined. In ventral view the parietal is laterally convex and transversely concave, with the sides becoming progressively steeper more posteriorly (Text-fig. 6B).

The parietal overlaps the frontals anteriorly ; the slightly concave suture surface bears strong ridges which become weaker laterally (Text-fig. 7B). The median process of the parietal fits between the frontals and is itself overlapped slightly (Text-figs. 5A, 6B). The antero-lateral corner forms a vertical facet with strong sutural ridges for the postorbital (Text-fig. 4B). The anterior part of the ventral edge is flat, then grooved (the laterosphenoid fitted against this region) while more posteriorly this edge is sharp (Text-fig. 6B). The parietal enclosed the dorsal part of the supraoccipital (Text-fig. 5A).

Frontal (F). The frontals are elongate and form most of the dorsal margin of the orbits. In dorsal view (Text-fig. 5B) the central part of each bone is slightly concave transversely. The orbital rim, which bears well-developed insertion markings, is quite thin because the ventral surface above the orbits is obliquely concave (Text-fig. A4) ; the plane of the orbital circle makes an angle of about 45 degrees with the mid-line (Text-fig. 7B). This obliquely concave surface forms a very prominent and sharp-edged ridge ventrally (Text-fig. 6B) where it meets another concave surface,

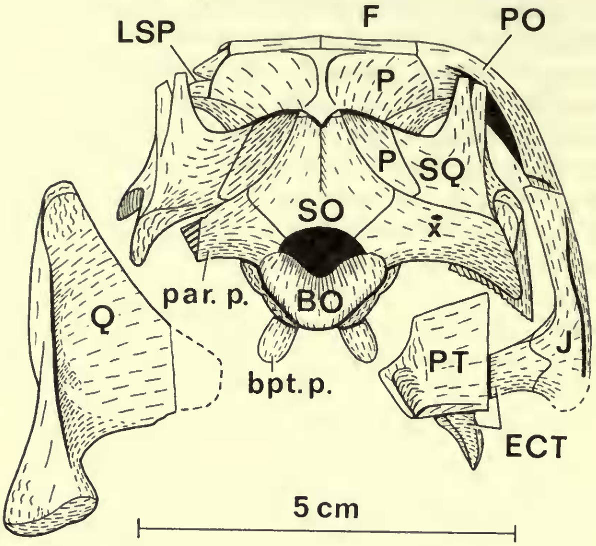


FIG. 8. *Hypsilophodon foxii.* Skull R2477, × 1. Abbreviations : bpt. p., basipterygoid process ; par. p., paroccipital process ; x, remnant of post-temporal fenestra. For other abbreviations see page 21.

the 'transverse' plane of which varies so that the curve is always perpendicular to that of the orbital surface. This medial curved surface is more strongly concave anteriorly.

The sutural markings on the thin anterior part of the edge between the frontals are very slight but on the thick central part they are well developed, consisting of a cone-within-cone pattern (Text-fig. 5A). On the thinner posterior part they are deeper, more vertical but less regular. The frontals are sutured to the parietal, the prefrontals and the squamosals. Postero-laterally on the ventral surface there is a slight depression which, together with the larger one on the postorbital, receives the head of the laterosphenoid (Text-fig. 6B). The postorbital itself sutures on to a well-developed spike (Text-fig. 7B) of the frontal.

Jugal (J). The outer orbital edge of the jugal is gently rounded and medial to this the jugal floors the ventral part of the orbit (Text-fig. 5B). Anteriorly this floor is obliquely inclined, facing medially and somewhat postero-dorsally but posteriorly the plane shifts until it faces anteriorly (Text-fig. 7A). The inner edge of this orbital floor is rounded anteriorly but becomes very thin and sharp-edged more postero-dorsally (Text-fig. 4B). The remainder of the jugal is an extremely thin sheet of bone. Anteriorly the jugal fits against the ventral edge of the thick part of the lachrymal. The sutural relationships with the maxilla and lachrymal vary in R197 (Text-fig. 2A) and R2477 (Text-fig. 4A). Posteriorly the jugal forms an 'M'-shaped suture with the pointed ends of the maxilla and ectopterygoid (Text-fig. 6A). The postero-dorsal part of the jugal has an overlapping suture with the tapering end of the postorbital (Text-fig. 4A). The thin part of the jugal overlaps the quadratojugal (Text-fig. 2A).

Quadratojugal (QJ). The sheet-like quadratojugal is perforated by a relatively large foramen (Text-fig. 2A). The edge of this foramen and the ventral edge of the bone are rounded while the dorsal and posterior edges are thinner and sharp. The anterior edge is hidden by the overlapping jugal. Postero-dorsally the quadratojugal is overlapped by the quadrate but more ventrally the position is reversed, with the quadratojugal extending nearly to the mandibular condyle (Text-figs. 3, 4A).

Quadrate (Q). From its rounded condylar region the main body of the quadrate rises, twisting through 45 degrees, to form a head (Text-fig. 4A). This head, triangular in cross-section, inserts in a socket in the squamosal ; its anterior (Text-fig. 7B) and inner (Text-fig. 5A) surfaces are covered with markings of ligamentous insertions. The main body of the quadrate and its pterygoid flange, set at about 70 degrees to one another, form the outer (Text-fig. 3) and the posterior (Text-fig. 7A) borders respectively of the lower temporal vacuity. The anterior and posterior edges of the main body of the quadrate are thin and sharp but its shaft is thicker and more rounded. For most of its height the pterygoid flange arises from the middle of the main body but dorsally its origin migrates backwards and takes part in the formation of the dorsal head of the quadrate (Text-figs. 5A, 8). A process of the squamosal fits between these two sheets of the quadrate in this region. The junction region between these two sheets is laterally concave along most of its length posteriorly (Text-fig. 8) and also anteriorly (Text-fig. 7B), but here the angle is more acute. The antero-medial face of the shaft is slightly concave dorso-ventrally (Text-fig. 7B) with well-developed pore markings.

There is very extensive overlap between the pterygoid flange and the alar process of the pterygoid. Neither of these two sheets is complete, but the shape of the missing parts of each is outlined on the more basal parts of the other. The quadratojugal has an overlapping suture with the lateral sheet of the quadrate and the limits of the suture are marked by an edge (Text-figs. 3, 4A).

Squamosal (SQ). This bone forms the postero-dorsal corner of the skull (Text-fig. 3), the lateral part of the occipital crest (Text-fig. 5B) and the posterior portion of the upper temporal bar. It is a roughly quadriradiate bone with rather unequally developed processes. The external surface (Text-fig. 4A) at the junction of the two larger processes, which are anteriorly and medially directed, is strongly convex while the inner surface (Text-fig. 7B) is concave forming the latero-posterior wall of the supratemporal fossa. Ventro-laterally there are two smaller processes which border the deep socket for the head of the quadrate. The posterior process forms a continuous sheet with the medial process and in posterior view (Text-fig. 8) the surface passing laterally is basically gently convex and then concave but dorsally above the socket there is a strongly convex part. In lateral view (Text-fig. 4A) there is an edge joining the lateral edge of the anterior process to the posterior edge of the posterior process (Text-fig. 5B). In ventral view (Text-fig. 6B), the large anterior concave area and the socket are separated by a wide bridge of bone, which shortly tapers as it passes antero-laterally and the surface of which is concave in this direction. The edges of the bone are thin and sharp. The medial process overlaps the

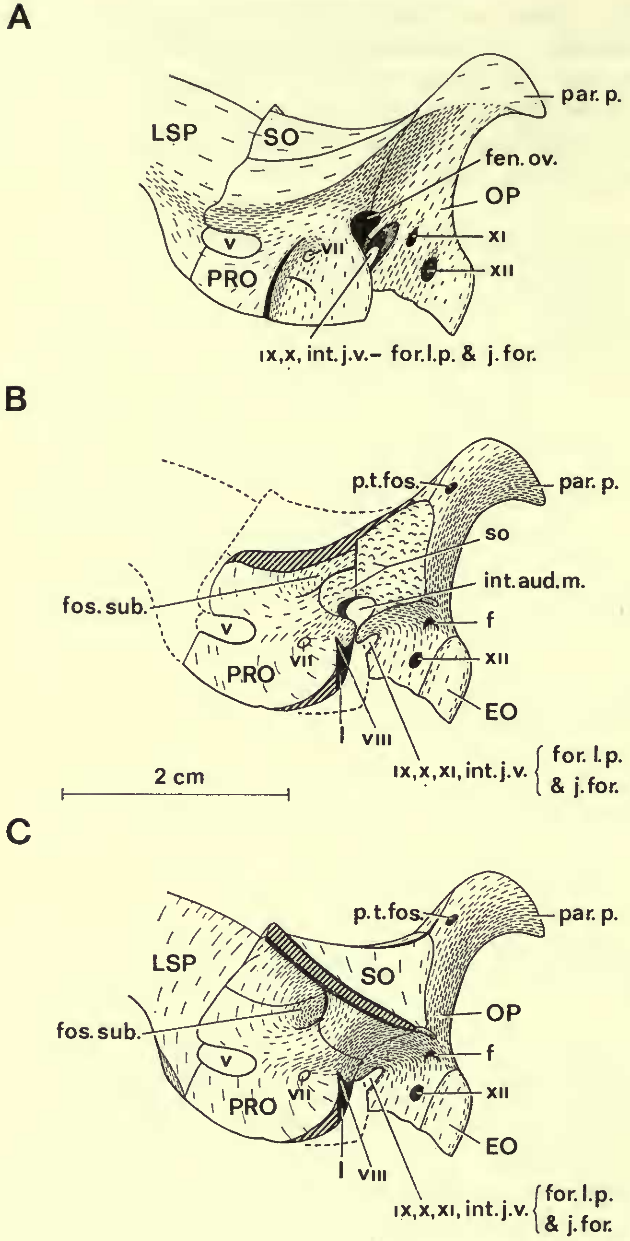


FIG. 9. *Hypsilophodon foxii.* Side-wall of braincase, composite : EO, exoccipital R8367 ; LSP, laterosphenoid R2477 ; OP, opisthotic R194, R2477 ; SO, supraoccipital R8366. × 1·5 for R2477. A, ventro-lateral view ; B, dorso-medial view with supraoccipital removed. C, as B but with supraoccipital sectioned. Abbreviations : f., foramen ; fen. ov., fenestra ovalis ; for. l. p., foramen lacerum posterius ; fos. sub., fossa subarcuata ; int. aud. m., internal auditory meatus ; int. j. v., internal jugular vein ; j. for., jugular foramen ; l., lagenar recess ; par. p., paroccipital process ; p.t. f., remnant of post-temporal fenestra ; so., surface for supraoccipital ; foramina for cranial nerves in Roman numerals, other abbreviations see Fig. 60

parietal anteriorly. The ventral edge of this process is sutured to the opisthotic while the posterior process is overlapped by the paroccipital process (Text-figs. 7B, 8). The anterior process is overlapped laterally by the posterior process of the postorbital.

Lachrymal (L). The main part forms the dorsal border of the antorbital fenestra while the medial sheet forms an inner wall (Text-fig. 3). In lateral view (Text-fig. 3) the main part is gently convex transversely and longitudinally. Ventrally it is hollowed out to form a thin and sharp edge which overhaps the base of the medial sheet. The plane of this sheet is at an angle to that of the main part so that they are wider apart posteriorly. Here the lachrymal has a posterior surface (Text-fig. 5B) which forms part of the margin of the orbit. The lachrymal foramen is on this surface and its duct follows the curved dorsal margin of the lachrymal in the junction region (Text-figs. 60C, D). It opens at the pointed anterior end medial to the maxilla. The sutural relationship with the maxilla and jugal varies in R197 (Text-fig. 2A) and R2477 (Text-fig. 4A). The end of the palatine bar sutures to the medial edge of the lachrymal just anterior to the jugal (Text-fig. 5B). Dorsal to this there is a groove along the postero-medial edge of the lachrymal (Text-fig. 4B) in which there is still a small piece of bone. The original bone was a slender rod. The dorsal edge of the lachrymal is sutured to the prefrontal and nasal ; this edge has a groove to receive the prefrontal while more anteriorly its edge fits into a groove on the edge of the nasal.

Prefrontal (PF). This bone forms the edge of the orbit and consists of two tapering sheets ; the dorsal one (Text-fig. 5B) is gently convex antero-posteriorly while the lateral one is concave (Text-fig. 4A), obliquely inclined and slightly twisted along its longitudinal axis. The medial surface (Text-fig. 5A) is concave but more gently angled and the long edges are sharp. The prefrontal overlaps both the nasal and the frontal (Text-figs. 5B, 6B). The anterior edge fits into a groove on the dorsal edge of the lachrymal. The lateral corner of the bone is thick with well-developed suture pits and ridges for the supraorbital.

Supraorbital (SOB). The supraorbital is preserved in the right orbit of R197 (Text-fig. 2B) and there is one from R194 (see Text-fig. 3). The shaft of the bone is curved and tapers, with an oval cross-section and sharp edges, and is slightly twisted along its longitudinal axis. Anteriorly there is a dorso-medial flange that is also present in R197 but there is no sutural area corresponding to it on the prefrontal of R2477. There is a transversely concave area on the outside of the flange with a slight ridge on the shaft. The dorso-lateral surface and the posterior part of the inner surface are covered with fine surface markings. More proximally it is smooth but with several slight ridges running diagonally across the shaft.

Postorbital (PO). This is a triradiate, sharp-edged bone forming the posterior wall of the orbit and the anterior part of the upper temporal bar. The outer surface is flat antero-posteriorly and curved transversely (Text-fig. 7B). The slender and tapering posterior and ventral processes (Text-fig. 5B) are in the same plane. The posterior process is thinner than the ventral, which latter has a medial ridge and is triangular in cross-section (Text-fig. 6B). This ridge becomes thicker dorsally where it forms the ventral part of the medial process (Text-fig. 6B). The medial process is short but stout with a dorsal ridge (Text-fig. 5B) which links a similar ridge on the parietal to the dorsal edge of the posterior process. The surface behind this edge is slightly concave and is continuous with the ventral surface with which it forms a twisted plane (Text-figs. 5B, 6B).

There is a very strong union between the medial process of the postorbital and the adjacent bones. Ventrally the thick medial process has two large cavities, one lateral and ventral to the other, which are partly separated by a thin dividing wall. The dorso-medial cavity is for the large spike on the corner of the frontal (Text-fig. 7B). This spike is bounded on all sides, though to a lesser extent ventrally, by the postorbital which also overlaps the frontal with a small anterior flange (Text-figs. 5B, 6B). The roof of the ventro-lateral cavity forms an oval depression (Text-fig. 6B) with the adjacent surface of the frontal. This depression, the side-walls of which become deeper as they pass laterally, is for the large head of the laterosphenoid (Text-fig. 7A). Posteriorly there is a small sutural surface for the parietal. The tapering end of the posterior process overlaps the anterior process of the squamosal while the ventral process overlaps the jugal (Text-figs. 3, 4A).

Pterygoid (PT). The triradiate pterygoid has long and thin alar processes to the adjacent bones. Those for the palatine and ectopterygoid form a sheet (Text-fig. 6A) which is slightly concave antero-posteriorly. Approximately perpendicular to this sheet, to which it is linked by a thickened connecting region, is the very broad alar process for the quadrate (Text-figs. 4B, 6A). In medial view (Text-fig. 4B) the quadrate process is concave dorso-ventrally apart from the obliquely convex antero-dorsal corner. Ventrally there is a concave border delimited by an edge that runs parallel to the ventral margin. The anterior part is thicker, covered with insertion markings and has a centrally situated depression. This depression with the adjacent small process receives the basipterygoid process of the basisphenoid (Text-figs. 5C, 6A). The lateral surface of the quadrate process has a well-defined sutural area (Text-fig. 4A) for the quadrate.

In ventral view (Text-fig. 6A) there is a well-defined corner on the centre of the connecting region. The anterior edge of the connecting region is sharp but becomes rounded at the base of the quadrate process (Text-fig. 7B). The anterior part of the palatine process is missing but the part of the palatine that was overlapped is visible (Text-fig. 6A). The pterygoid overlaps the ectopterygoid ventrally with a broad process which tapers to a point.

Ectopterygoid (ECT). The main part consists of a bar, triangular in cross-section, which forms two equal halves at right angles to each other (Text-figs. 5C, 6A, 7B) plus a medial flange (Text-fig. 5C). The dorsal ridge on the anterior half of the ectopterygoid is gently rounded with a convex surface in front of it (Text-fig. 5C). More medially and posteriorly this edge becomes thinner and sharper, with irregular bumps, and the surface medial to it is concave. In the central region this surface is large because it continues on to the medial flange (Text-fig. 5C). The other edges of the bone are thin and sharp. The lateral end of the ectopterygoid is strongly

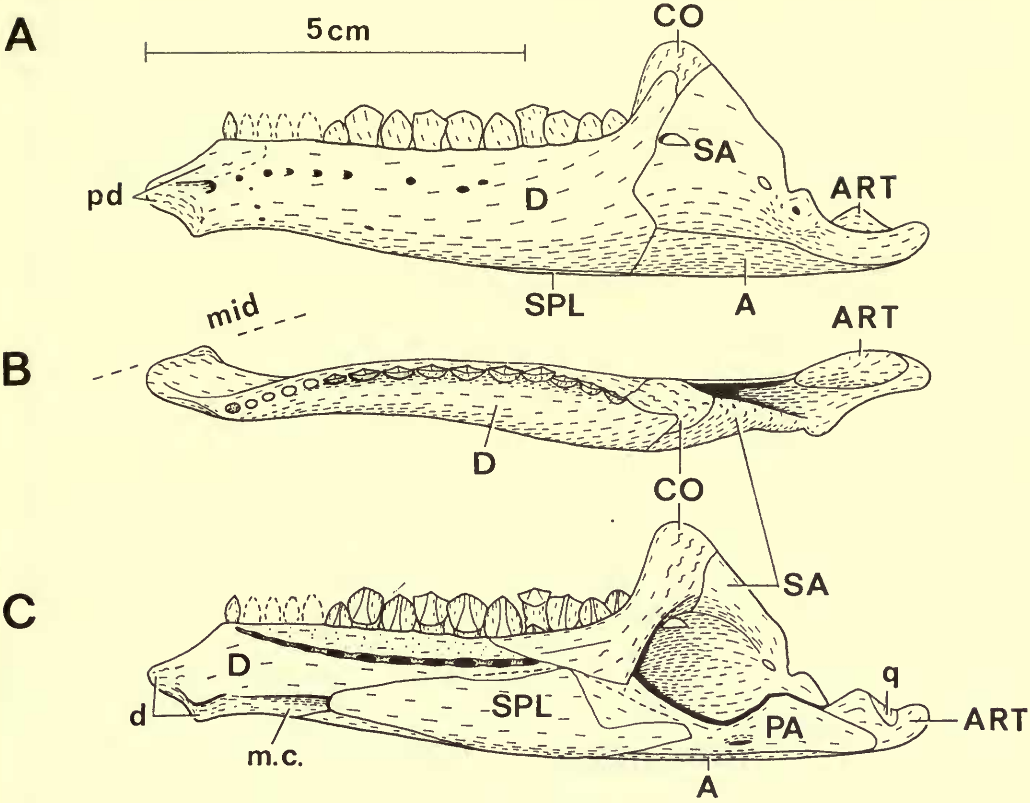


FIG. 10. *Hypsilophodon foxii.* Mandibular ramus, × 1 for R196 with details from R193, R197 and R2477. A, antero-lateral view; B, dorsal view; C, postero-medial view. Abbreviations: d., surface for dentary; m.c., Meckelian canal; mid, midline; pd, surface for predentary; q, surface for quadrate. For other abbreviations see page 21.

sutured to the jugal (Text-figs. 4B, 5, 6A, 8). The antero-ventral surface of the anterior half of the bone is excavated to form a deep groove for the sharp posterior edge of the maxilla (Text-figs. 5, 6A, 7B). The medial flange of the ectopterygoid is sunk into the dorsal surfaces of the pterygoid (Text-fig. 5C).

Palatine (PAL). The palatine consists of a broad base, sutured to the medial surface of the maxilla (Text-figs. 4B, 5A, C), and bears a thin alar process from approximately along the middle and perpendicular to the base (Text-figs. 5A, C). Dorsally and ventrally the surface of the palatine is continuous with the adjacent surface of the maxilla (Text-figs. 5C, 6A). Anteriorly the palatine is much thicker and set at about 70 degrees to the maxilla. The lateral end of this thick part of the palatine forms a bar, triangular in cross-section, which bridges the antorbital fossa to suture with the medial surface of the lachrymal (Text-figs. 5B, 5C). The dorsal surface (Text-fig. 5C) in slightly convex longitudinally and slightly concave transversely, with this

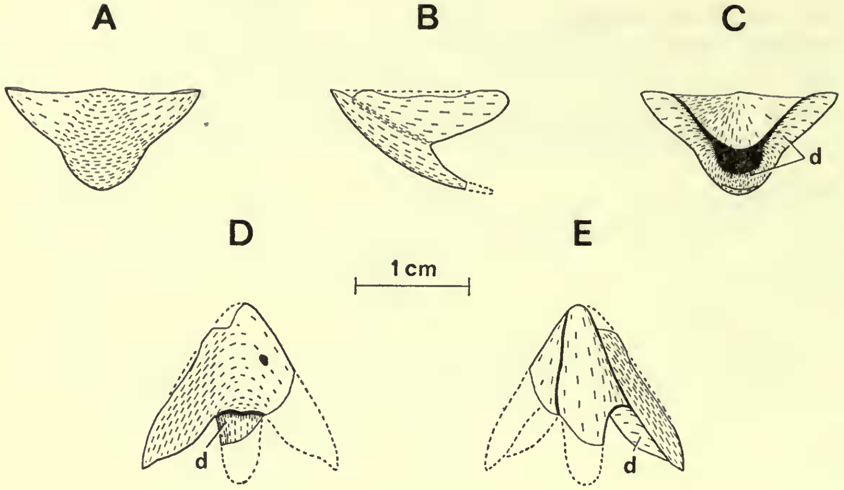


FIG. 11. *Hypsilophodon foxii.* Predentary R2470, × 1·5. A, anterior view; B, lateral view; C, posterior view; D, dorsal view; E, ventral view. Abbreviation: d, surface for dentary.

curve becoming stronger on the posterior part of the bone where the alar process is slightly convex (Text-fig. 4B). The thick anterior edge forms a surface, tapering medially, which is convex dorso-ventrally and straight transversely except for the medial part which is concave (Text-fig. 5C). In medial view (Text-fig. 4B) the bone is gently convex with a concave region where it joins the alar process. The curve continues on to the thicker anterior part of the process. Posteriorly the alar process overlapped the pterygoid. This sutural surface is bordered laterally by a thickened edge (Text-fig. 6A). The anterior end was probably sutured to the vomer. However, there is no definite sutural surface on the anterior part of the palatine which, like the posterior part of the vomer, is damaged and incomplete.

Vomer (V). The tapering head of this median bone is triangular in cross-section and fits between the maxillae (Text-fig. 6A). Ventrally the head sutured to the floor of the premaxillae and the posterior limit of this suture is marked by a step (Text-fig. 6A). Slightly behind the head there is a dorsal groove that was for the median cartilaginous septum. The groove becomes deeper as it passes posteriorly so that the rest of the vomer consists of two thin sheets separated dorsally and curving out laterally (Text-figs. 5C, 6A). Laterally there is a longitudinal ledge (Text-fig. 4B), the dorsal surface of which is convex dorso-ventrally while the ventral surface is concave. This ledge was probably for the anterior part of the palatine. Ventral to this ridge in R194 there is a foramen, the ventral margin of which has been lost in R2477 (Text-fig. 4B).

The lower jaw consists of seven bones and the two rami are linked anteriorly by the median predentary. Only one *predentary* (PD) is known (Text-fig. 11) and this was preserved next to the dentary (see Nopcsa 1905, fig. 3). The dorsal surface

(Text-fig. 11D) is gently concave transversely while postero-medially the surface is convex antero-posteriorly. The dorsal edge is sharp. The sides are gently convex with a groove running diagonally back from the anterior end (Text-fig. 11B). The paired lateral processes overlap the adjacent lateral surface of the dentaries (Text-figs. 3, 10A). Passing medially each process overlaps the dorsal edge of the dentary to a progressively greater extent so that the anterior tip fits into a groove on the posterior surface of the predentary (Text-fig. 11C). The symphysial region is also overlapped by the ventral process of the predentary ; the process is thin and transversely curved (Text-figs. 11D, E).

Dentary (D). In lateral view (Text-fig. 10A) the spout-like anterior end of the dentary is longitudinally convex but the rest of the bone is concave, the surface sweeping gently postero-laterally. The corresponding curves on the medial surface (Text-fig. 10C) are concave and then convex. The two rami diverge posteriorly, each becoming progressively deeper and thicker, the additional thickness being lateral to the tooth row (Text-fig. 10B). The transverse curve of the lateral surface becomes more convex posteriorly while, apart from the ventral Meckelian canal, all the medial surface (Text-fig. 10C) is gently convex. This canal ends just behind the symphysis and is deeper posteriorly, with the dorsal part enclosed by an edge from the dentary. The splenial covered most of this canal ; the canal carried the mandibular artery and vein plus the palatine ramus of the trigeminal nerve as in modern lizards (Romer 1956). About half-way along the dentary the canal opens into the adductor fossa, which greatly increases in depth (Text-fig. 12) and width posteriorly. Close to the symphysis the ventral edge is sharp ; the rest is rounded. There are several foramina along the lateral surface of the dentary which may have transmitted nerves and nutrient blood vessels to the lips. The most anterior and largest of these foramina probably represents the mental foramina through which a branch of the fifth nerve emerged (Gilmore 1909).

Anteriorly the two dentaries meet at a median and somewhat obliquely inclining contact surface (Text-figs. 10B, C). The splenial and coronoid overlap the dentary medially (Text-fig. 10C). The part of the dentary overlapping the angular and surangular (Text-fig. 10C) is thin but the part touching the coronoid is thick with strong sutural markings.

Splenial (SPL). This is thin and was applied to the inner surface of the mandibular ramus (Text-fig. 10C). It is gently convex longitudinally and more strongly so transversely, especially the ventral part that wraps round the ventral edge of the ramus and is visible in lateral view (Text-fig. 10A). This ventral edge is thick and rounded ; the other edges are thin and sharp.

Angular (A). This is thin and tapering (Text-fig. 10A) and the ventral part is transversely convex. Dorsally it overlaps the surangular (Text-fig. 10A) while ventromedially it overlaps the prearticular and part of the articular and is itself overlapped by the splenial (Text-fig. 10C).

Surangular (SA). This is thin and in lateral view (Text-fig. 10A) is transversely convex ; longitudinally the dorsal part is gently convex, the ventral part gently

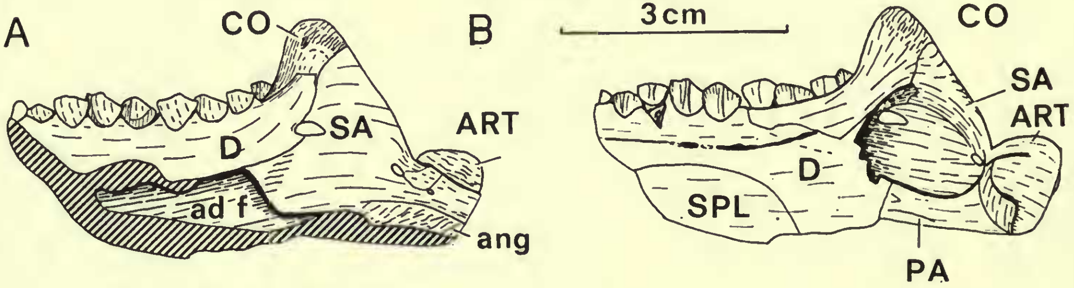


FIG. 12. *Hypsilophodon foxii*. Mandibular ramus R2477, ×1. A, lateral view; B, medial view. Abbreviations; ad. f., adductor or supramandibular fossa; ang., surface for angular. For other abbreviations see page 21.

concave. There are three foramina through the bone, two smaller ones posteriorly and one large one anteriorly, which were probably for the cutaneous branches of the inferior alveolar nerve as in modern lizards (Oelrich 1956). The most dorsal part of the anterior edge fits into a groove in the coronoid. The dorsal edge is thick, especially close to the coronoid. This edge also forms a well-developed boss just in front of the articular. The part overlapping the articular is thick and roughly oval in cross-section with a rounded dorsal edge.

Prearticular (PA). This is flat, tapers posteriorly and overlaps the dentary and is itself overlapped by the splenial and the coronoid (Text-fig. 10C). The ventral edge is overlapped by the angular. The prearticular then widens out again. The posterior part consists of two transversely convex curves separated by a thin slit (Text-fig. 10C) through which the chorda tympani branch of the seventh nerve probably passed as in other reptiles (Romer 1956). More posteriorly the bone becomes transversely convex and then flat and overlaps the articular.

Articular (ART). The articular is roughly triangular in lateral view with one apex dorsal in position (Text-fig. 10A). The rounded anterior edge is thin but the rest of the bone is much thicker. The ventral edge forms a flat surface while the posterior edge, which is concave in lateral view (Text-fig. 10A), is gently convex transversely and formed the articular surface for the quadrate. The articular is overlapped laterally by the surangular, ventrally by the angular and medially by the prearticular.

ii) TEETH AND TOOTH REPLACEMENT

Dental formula. There are five teeth on each premaxilla (Text-figs. 2, 4). The number of maxillary teeth is ten (Text-fig. 6A, left side) or eleven (R197, R2477, Text-fig. 6A and R5862, Swinton 1936, fig. 1). The predentary is toothless and the number of teeth borne by the dentary is not certain as the dentaries of R197 and R2477 are incomplete anteriorly. In R8366 the anterior part of the dentary is preserved and this bears four smaller alveoli at the front. In R2470 the roots of teeth are preserved in these four smaller alveoli. In R196 (Text-fig. 10) the complete dentary is preserved but it is slightly damaged and some of the teeth are missing; the most anterior of the smaller teeth is preserved and, assuming that there were three more, the original count would have been 14. In the large individual R192, the anterior part of the jaw is missing but there are 13 teeth of which only the most anterior is small. A complete dentary is needed to show the number of teeth but there were certainly more than on the maxilla, not less as believed by Hulke (1882) and Parks (1926).

Premaxillary teeth. The five premaxillary teeth are preserved *in situ* on the left side of R197 (Text-fig. 2A). In the toothless premaxilla R8367 the sockets for the teeth are visible and these closely resemble those of the maxilla as figured by Swinton (1936, fig. 1). A loose tooth is figured by Hulke (1882, pl. 72, figs. 3–4) and one from R196 in Text-fig. 13. The root is separated from the head by a slight constriction and is circular in cross-section. The root is open with a large pulp cavity which extends into the crown (Hulke 1882). The crown is slightly compressed laterally

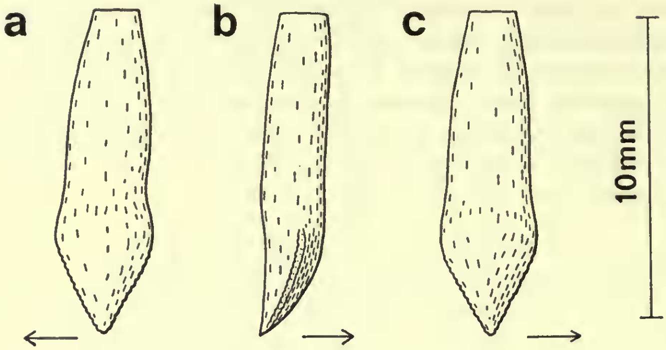


FIG. 13. *Hypsilophodon foxii.* Predentary tooth R196, × 4. a, lateral view; b, anterior view; c, medial view. Arrow in text-figs. 13 to 16 points anteriorly or laterally depending on the view.

with the outer surface of its cross-section less convex than the inner. The pointed crown has sharp edges anteriorly and posteriorly which bear a series of fine serrations. On the medial surface (Text-fig. 13c) there is a slight depression running diagonally towards the tip on each side. Both surfaces are smooth – that of the root is rather matt while that of the crown is very shiny and obviously thickly enamelled on both sides (visible in section of R2472). There are several minute striae on both sides of the crown.

Maxillary and dentary teeth. These are preserved in skulls (Text-figs. 2, 6A, 12) and loose teeth were figured by Hulke (1873, pl. 18, figs. 4–6; 1882, pl. 72, figs. 5–9), Swinton (1936, figs. 2–3) and in Text-figs. 14–16. The crowns of both types are laterally compressed and wider than the root, which is cylindrical and tapering. One side of the crown (the lateral side of the maxillary teeth and the medial side of the dentary teeth) is covered with a thick layer of enamel and bears several longitudinal ridges. On the upper teeth these ridges are all weak but on the lower teeth the central ridge is extremely well developed. The other side of the tooth is smooth and shiny. Ground sections show that there is a thin layer of enamel on unworn teeth (R8419), as Swinton (*in* Sternberg 1940) suggested, and in worn teeth (R2472) as well. In the section of the unworn dentary tooth R8419, in which the width of the crown is 5·5 mm, the medial enamel layer at 0·1 mm is about five times as thick as the lateral layer. The thickly enamelled edge of the tooth was more resistant to wear and formed a sharp edge to the worn surface of the tooth. The obliquely inclined occlusal surface of some teeth is gently concave transversely and flat longitudinally.

Maxillary teeth in longitudinal section curve slightly medially (Text-fig. 14a). The root is about twice as long as the unworn crown. A depression runs along the anterior edge of about half of the root and continues a little way on to the crown (Text-fig. 14A). The crown of each tooth slightly overlaps the tooth behind and fits against this anterior depression. The boundary between the root and the crown is formed by a slight cingulum. The crown is laterally compressed and, apart from the

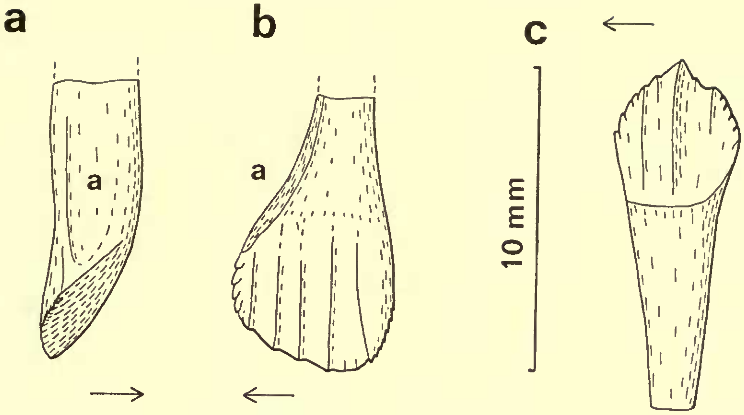


FIG. 14. *Hypsilophodon foxii.* Unworn maxillary tooth R8367, ×4. a, anterior view; b, lateral view; c, unworn dentary tooth right side R8367, ×4, lateral view. Abbreviation: a, depression for the more anterior tooth.

slight longitudinal ridges, the outer thickly enamelled surface is flat; the inner surface is very slightly concave longitudinally, gently convex transversely. In an unworn tooth the rounded apex is somewhat posterior to the centre of the crown. The number and degree of development of the longitudinal ridges on the enamelled lateral surface of the crown varies. There are usually three ridges which reach the cingulum: an obliquely inclined ridge on the antero-dorsal edge of the crown, another from the apex and a third close to the posterior edge of the crown. Extra ridges may be developed on the wider anterior part between the oblique ridge and the apex ridge. Up to three ridges may be present and may or may not reach the cingulum. The anterior edge bears several small crenellations and there are a few others between the apex and the posterior ridge. There are numerous faint longitudinal ridges on the thinly enamelled medial side.

Dentary teeth (Text-figs. 15, 16) are orientated in the reverse way to those of the maxilla. The ridged and thickly enamelled surface is medial, instead of lateral; the tooth curves laterally, instead of medially; more of the crown is posterior, instead of anterior to the apex and the oblique ridge is posterior instead of anterior. The cingula of dentary teeth are more strongly developed, the apices are more pointed and more central on the crowns. However, the striking difference is the prominent development of the apical ridges of the dentary teeth. The other longitudinal ridges are faint, resembling those of the maxillary teeth, but the apex ridge is very large and forms a well-developed 'spike' as the crown is worn. In large teeth there may be several fine longitudinal ridges on the lower half of the apex ridge. The degree of development of the anterior ridge varies and it may be practically absent. The number and lengths of the ridges developed between the apex and the posterior oblique ridge vary: there may be an anterior long one plus a short one, or just an anterior short one. The anterior and posterior edges both have numerous fine crenellations.

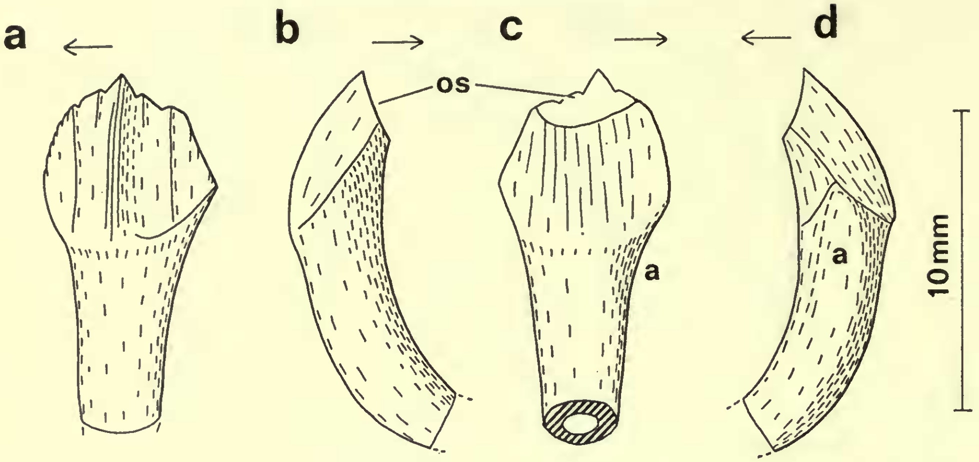


FIG. 15. *Hypsilophodon foxii*. Worn dentary tooth, right side, R8367, × 4. a, medial view; b, posterior view; c, lateral view; d, anterior view. Abbreviations: a, depression for the more anterior tooth; os, occlusal surface.

Special foramina and replacement teeth. On the medial surface of the maxilla above the tooth row there is a series of foramina connected by a shallow groove (Text-fig. 5A). Each foramen corresponds to a tooth position and is situated directly above it. The edges of the foramina are straight ventrally and gently concave dorsally. The bone surface between the foramina and the tooth row is pitted. The foramina open into the alveoli of the functional teeth. A comparable series is present on the dentary (Text-fig. 10C). In certain cases (maxilla of R5862 and R6372, dentary of R2477 and R8366) a replacement tooth is visible through a foramen.

Edmund (1957) discussed the function of the special foramina in ceratopsians and hadrosaurs. He concluded that these foramina were for the admission of parts of the dental lamina or for the admission of young replacement teeth produced by the lamina. Edmund (1957 : 13) noted that the foramina 'are not seen in primitive forms, are seen in some of the more advanced forms, and are best developed in forms with very high alveolar walls. This definitely points to their function as orifices for the admission of dental germinal material.' While not disputing Edmund's conclusion concerning the function of these foramina, it should be noted that they are well developed in *Hypsilophodon* (Text-figs. 5A, 10C), *Dysalotosaurus*, *Camptosaurus* and *Iguanodon* (see Galton in press). Their absence in other lower ornithopods is probably more apparent than real and reflects the state of preservation of the material. These foramina represent a *preadaptation* for the development of a dental battery consisting of vertical tooth series, because high alveolar walls can be developed (Galton in press). This potential was realized independently in two lines of ornithischians, the hadrosaurs and the ceratopsians.

In *Hypsilophodon* a small replacement tooth is preserved in the alveolus where it is closely applied to the medial surface of the functional tooth. At a later stage in

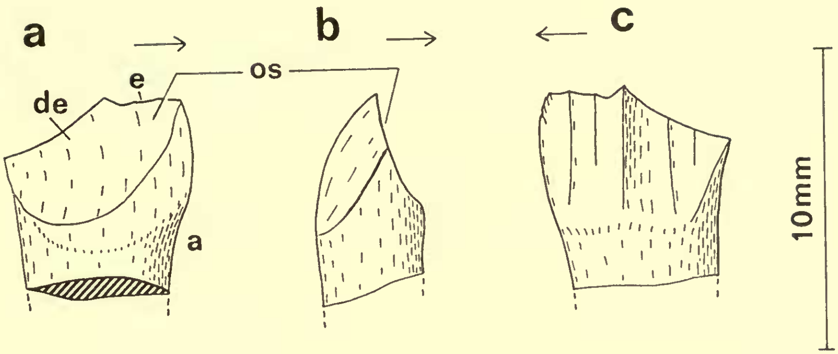


FIG. 16. *Hypsilophodon foxii.* Well-worn dentary tooth, right side, R8367, ×4. a, lateral view; b, posterior view; c, medial view. Abbreviations: a, depression for the more anterior tooth; de, dentine; e, enamel; os, occlusal surface.

its development the replacement tooth is more lateral in position because it is underneath the functional tooth. When this situation is visible, as in the dentary of specimens R192, R196 (Text-fig. 10C) and R2477 (Text-fig. 12B), the root of the functional tooth is much shorter than the original length of the crown. Resorption of the root must therefore have occurred because in an unworn tooth the root is about twice as long as the crown. A functional tooth in this condition was readily shed so that the replacement tooth could continue growing upwards into its position.

In the case of the premaxilla the bone medial to the tooth row is obliquely inclined (Text-fig. 5B) rather than vertical as in the maxilla and dentary. However, the situation is similar because the replacement tooth is close to the medial surface of the functional tooth and lateral, but also ventral, to the foramina. There are five premaxillae with teeth – 24 preserved in all – but only one case (R5830) preserves a non-functional replacement tooth in the alveolus.

Sequence of tooth replacement. In a study of tooth replacement in reptiles Edmund (1960) found that all the teeth with 'odd' numbers in a numbered tooth series are replaced in sequence, followed by all the 'evens'. The pattern of waves of tooth replacement in most cases pass anteriorly so that the teeth of each 'odd' or 'even' series erupt progressively from back to front. In *Hypsilophodon* this general pattern is discernible in the tooth rows of the premaxilla, maxilla and dentary. It is especially clear in the right maxilla of R2477 in which ten teeth (Text-fig. 6A) are well preserved. If the youngest tooth and the most worn tooth are designated as stages 1 and 6 respectively, then the stage of eruption of the remaining teeth can be assessed on this scale (Table IV). Apart from the first tooth, the teeth in the right maxilla clearly show that replacement is alternate, with replacement waves passing anteriorly. Both 'odd' and 'even' tooth series show two replacement waves – the junction of those of the 'odd' series is between tooth 3 and 5 and that of the 'even' teeth between 8 and 10. The first tooth is out of sequence as is also the case on the left maxilla (likewise the last tooth of the dentary); these teeth, however, are small and have no wear surfaces. The replacement sequence of the premaxillary teeth of R2477 is not apparent. In specimen R8367, however, where the functional teeth have been lost, there are replacement teeth in the medial part of sockets 1, 3 and 5 but not in 2 and 4, so here too the replacement appears to have been alternate.

Table IV

Stages of eruption of teeth at various positions along the jaw in R2477

Tooth position	1	2	3	4	5	6	7	8	9	10	11	12	13
a) Left maxilla	6	x	x	6	5	2	5·5	5	2	5·5	4·5	–	–
b) Right maxilla	1	3·5	5	4	2	5	3	6	5	2·5	–	–	–
c) Right dentary	x	x	x	x	5·5	2·5	6	3	2	5	2	6	1

iii) ACCESSORY ELEMENTS

Hyoid apparatus. In specimens R192 and R196 there are remains of a slender element preserved medial to the mandibular ramus. In R196 this element is gently curved along its length and transversely flattened – it is about 2·5–3·0 mm wide and more than 40 mm long, being broken at both ends. In R197 (Text-fig. 2C) the edges are more rounded while in R192 the small pieces that are preserved on both sides are definitely rod-like. These are regarded as the first ceratobranchial because this is the dominant and most highly ossified element of the hyoid apparatus in modern reptiles (see Ostrom 1961).

Sclerotic ring. Hulke (1873 : 523), when referring to an individual *in situ* in marl (remains as specimens R2466–76), noted that in the orbit there were 'several small osseous scales which [he] judged to be vestiges of a sclerotic ring'. Subsequently (1874, 1882) he figured the 'thin bony scales' of another specimen, R2477. Nopcsa (1905) reinterpreted this specimen correctly and showed that the sclerotic plates were the wear surfaces of the dentary teeth. He therefore concluded that there was no sclerotic ring in *Hypsilophodon*. Hulke's original observation (1873) on R2466–76, however, has been confirmed by the further preparation of the skull material. Further, a nearly complete sclerotic ring is preserved in one orbit of R2477 (Plate 1, fig. 3) with several plates in the other orbit. Plates are also preserved in R192 and R197 (Text-fig. 2B).

The presence of a sclerotic ring in *Hypsilophodon* is not surprising because it has been found in several dinosaurs (Edinger 1929, Ostrom 1961) and in *Parksosaurus* (Galton, in press, fig. 1). Where it can be determined, the sclerotic pattern of dinosaurs conforms to pattern A of Lemmrich (1931), with two positive plates and two negative plates. The ring is divided into four quadrants which are not necessarily equal in size. The positive plates are dorsal and ventral in position and overlap another plate at both ends. The negative plates are anterior and posterior in position and are overlapped by another plate at both ends. The sclerotic ring of *Corythosaurus* (see Ostrom 1961) and *Lambeosaurus* (see Russell 1940) consists of 14 plates while in *Anatosaurus* there are 13 plates (see Edinger 1929).

The sclerotic ring of *Hypsilophodon* consists of 15 plates (Text-fig. 17). The anterodorsal quadrant has been eliminated because the dorsal positive plate overlaps the

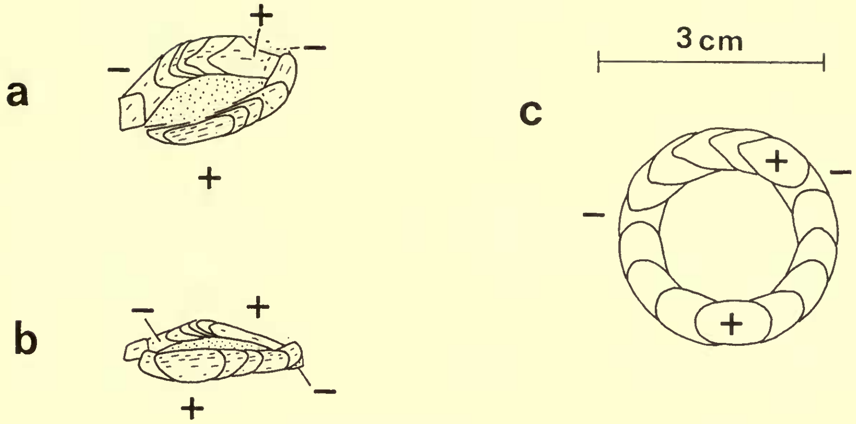


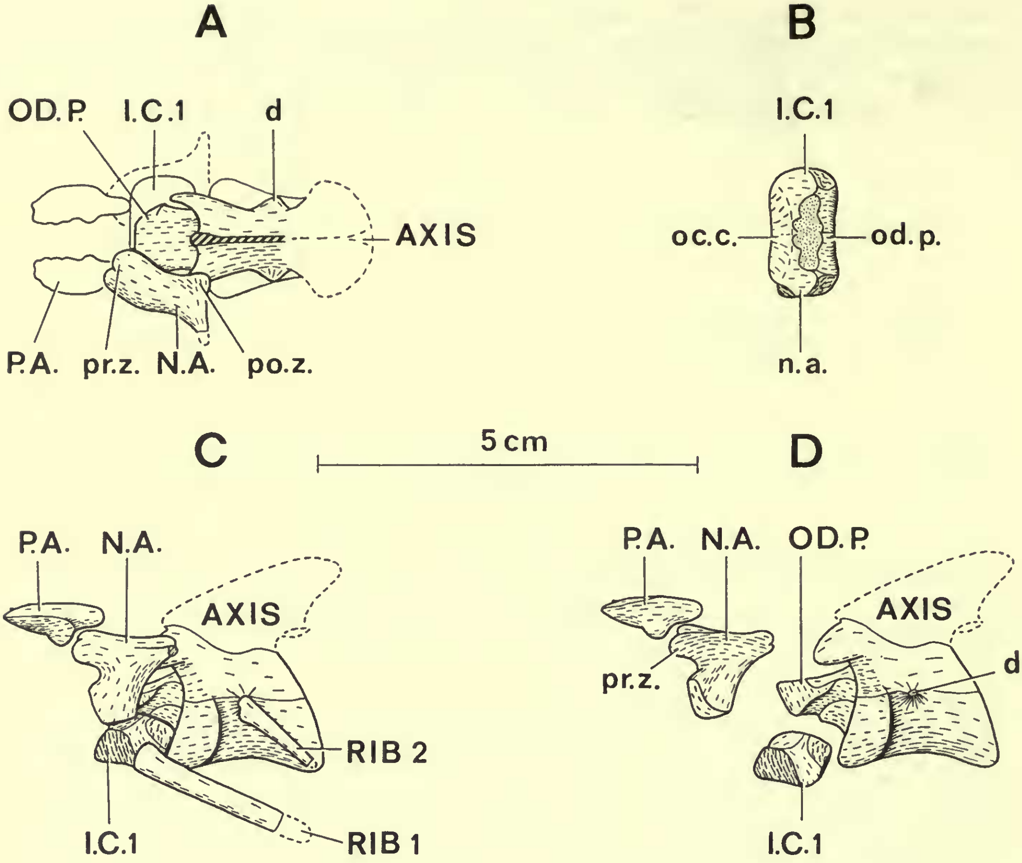
FIG. 17. *Hypsilophodon foxii.* Sclerotic ring R2477, × 1. a, lateral view ; b, ventral view ; c, reconstruction.

anterior negative plate with no intervening plates. Although not previously reported in dinosaurs this condition is known in several birds including all the members of the family Phasionidae (partridges and pheasants ; Lemmrich 1931). The antero-ventral quadrant has four intervening plates ; the postero-ventral quadrant has three and the postero-dorsal quadrate has four.

The individual plates of the ring are gently convex longitudinally. In cross-section the outer part is gently convex and the middle and inner parts are gently concave. In R197 (Text-fig. 2B) there is an isolated plate which is sub-rectangular in outline with rounded edges ; this appears to be a positive or a negative plate. The long edges of the individual plates in R2477 are damaged but the overlapping part of each plate in the postero-dorsal quadrant clearly tapers to a point. This is not shown by the other plates but a comparable difference is shown in the ring of *Sphenodon* (Edinger 1929, fig. 23).

The length of the longest plate as preserved in R2477 has been used as the length of the individual plates in the reconstruction. An overlap of about a half has been assumed because this appears to be the amount of overlap between adjacent plates in birds and reptiles (see Edinger 1929, Lemmrich 1931). The sclerotic ring is shown overlapped by the supraorbital, but this may not be correct. As reconstructed the diameter of the ring may be too large if some of the plates were smaller than the one measured. In addition the degree of overlap may have been greater than half ; it certainly is as preserved but this may be a post-mortem effect. The overlap would also be reduced if, as was probably the case, the sclerotic ring were placed more ventrally in the orbit than in the reconstruction.

Stapes. Unfortunately no trace of a stapes was found in the prepared skulls. However, it is reasonable to assume that it was a rod-shaped element which, as in hadrosaurs (Ostrom 1961), ran from the fenestra ovalis to a tympanum supported between the quadrate and the paroccipital process.



b) *The vertebral column and ribs*

The vertebral column can be assembled from specimens R196 and R196a. The complete presacral series consists of 24 vertebrae – 9 cervicals and 15 dorsals. There are 6 sacral and about 45 to 50 caudal vertebrae.

i) PROATLAS, ATLAS AND AXIS

Proatlas. That of R2477 is presumed to be the left but this, together with the orientation shown in Text-fig. 18G, is only tentative. The proatlas of R196 is only two-thirds the size of that of R2477 although the atlas and axis are slightly larger.

Atlas. This consists of an intercentrum, an odontoid process and two neural arches. The intercentrum (Text-fig. 18) is a subcrescentic bone which anteriorly has a large shallow depression for the occipital condyle (oc.c. Text-figs. 18B, H). This depression is obliquely inclined with a sharp edge ventrally. More laterally

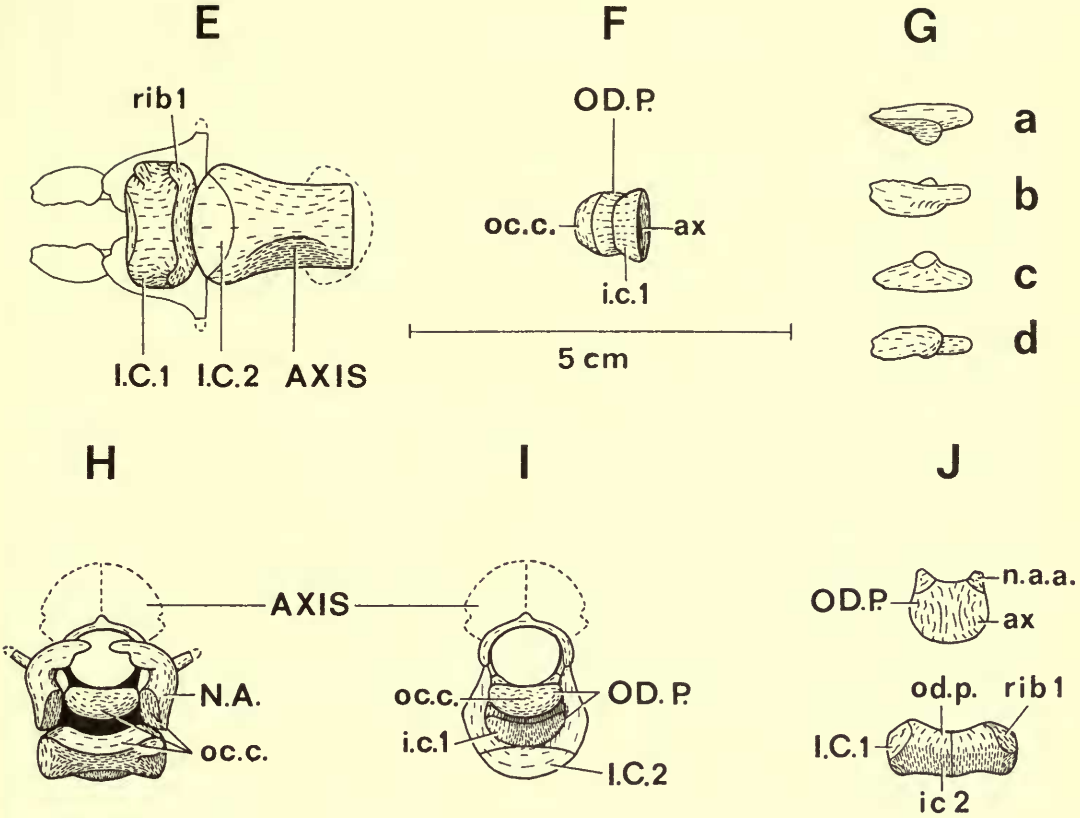


FIG. 18. *Hypsilophodon foxii*. Proatlas, atlas and axis R2477, × 1. A, dorsal view, right neural arch removed; B, atlas intercentrum, dorsal view; C, lateral view with ribs (rib 2 from R196); D, proatlas with atlas in medial view, axis in lateral view; E, ventral view; F, odontoid process of axis in ventral view; G. proatlas, view a = C, b = A, c = D, d = E; H, anterior view; I, axis in anterior view; J, odontoid process and intercentrum of axis in posterior view. Abbreviations: IC. 1, intercentrum of atlas; IC. 2, intercentrum of axis; OD.P., odontoid process of axis; P.A., proatlas; N.A., neural arch of atlas; RIB 1 and 2, ribs of atlas and axis; ax., surface for axis; d, diapophysis; i.c., surface for intercentrum; n.a., surface for neural arch of atlas; n.a.a., surface for neural arch of axis; oc.c., surface for occipital condyle; od.p., surface for odontoid process; po.z., postzygapophysis; pr.z., prezygapophysis; rib 1., surface for rib of atlas.

there are two surfaces, facing antero-dorsally and laterally, for the neural arches (n.a. Text-figs. 18B, C, D). The central part of the dorsal surface is sunken with an irregular though symmetrical outline (Text-fig. 18B). Ventrally (Text-fig. 18E) the surface is concave antero-posteriorly, forming a distinct edge with the anterior and posterior articular surfaces. Posteriorly, this surface medial to the rib facet is concave transversely but the remainder of the surface is convex. This ventral surface is covered with well-developed insertion markings. On the left side the anterior corner has a very irregular appearance (see Text-fig. 18E) which is not due to breakage and must be an individual variation.

The dorsal surface of the odontoid process is transversely concave next to the axis but becomes planar anteriorly (Text-fig. 18J). The ventral surface of the wedge-shaped odontoid is transversely convex. The anterior crescentic area is flat apart from a slight median depression (oc.c. Text-fig. 18H) with which the occipital condyle articulated. The base is gently concave and the intercentrum articulated with this surface (i.c. 1 Text-fig. 18I). Between these two surfaces and forming an obtuse edge with each there is a concave area which, after a slight constriction, passes on to the lateral surface to form a shallow depression (Text-fig. 18D). There is a sharp edge antero-dorsally but more posteriorly the surface is indented slightly with a gentle convex curve (Text-figs. 18A, D).

The neural arches (or neurocentra) are rather irregularly shaped bones which did not meet each other dorsally. Ventrally there are two articular surfaces (Text-fig. 18D) ; the larger posterior surface across the thicker part of the bone is for the intercentrum, the other faces slightly medially and contributes to the articulation for the occipital condyle (oc.c. Text-fig. 18H). Above these facets the outer surface is convex (Text-fig. 18C) and the inner slightly concave (Text-fig. 18D). On the outer surface where the shaft is constricted there is a well-defined bump. Anteriorly the region of the prezygapophysis forms a thin, curved sheet with two lobes (Text-fig. 18A). The postzygapophyseal process is slender and directed postero-dorsally and laterally (Text-figs. 18A, H). Medial to this the dorsal surface is concave. The ventro-medial surface is concave apart from the flat postzygapophysis, facing ventro-medially.

The atlantal rib (Text-fig. 18A) is long, laterally flattened and oval in cross-section. The head, which articulated with the intercentrum, is slightly expanded with an obliquely inclined concave surface. In R196 there is another single-headed rib next to the axis but it is slenderer than the atlantal rib of R2477 which is a smaller animal. It has also, close to its head, a small ventral plate which is presumably the remains of the capitulum (Text-fig. 18C) ; it is probably the axial rib because the rib of the third cervical vertebra was in position (Text-fig. 19).

Axis. The centrum is plano-concave with a shallow posterior depression. Anteriorly there is an oval intercentrum (Text-fig. 18E), triangular in sagittal section, with a sharp anterior edge. The neural arch has a well-developed and laterally compressed neural spine (Text-fig. 18A) which posteriorly is laterally expanded to form a frill-like plate (Text-figs. 18H, 20B). The ventral part of this plate is thicker and bears postzygapophyses which face ventro-laterally and slightly posteriorly. Anteriorly the neural spine is slightly thickened to form a projecting knob (Text-fig. 20B). The prezygapophyses are transversely convex and the postzygapophyses of the atlas articulated round their lateral surface. The ventral edge of the prezygapophysis continues on to the neural arch as a ridge below which the surface of the neural arch is concave (Text-fig. 18D). This concave area is continuous with the depression on the side of the odontoid process. The diapophysis (d. Text-fig. 18D) is small and is traversed by the rather indistinct suture between the neural arch and centrum. There does not appear to be a corresponding parapophysis on the centrum but this region is slightly damaged. However, it was probably absent because the rib of the axis appears to have been single-headed.

ii) CERVICAL VERTEBRAE 3 TO 9

The centra of cervical vertebrae 3 to 7 are opisthocoelous while those of 8 and 9 are amphicoelous. The centrum of the third cervical vertebra is laterally compressed; anteriorly there is a sharp ventral edge which widens out posteriorly where it is covered with well-developed surface markings. The remainder of the centra are also laterally compressed but ventrally the lateral surface curves outwards again to form a thickened keel (Text-figs. 19, 20A). The rounded ventral surface of this keel is covered with strongly developed and irregular surface markings.

The neuro-central suture bisects the parapophysis and is clearly visible in all cervicals (Text-fig. 19). The parapophyses of cervical vertebrae 8 and 9 are the largest. The diapophysis shows a progressive increase in robustness and length. In the fifth cervical it runs into the base of the prezygapophysis, in cervical vertebrae 6 to 9 the diapophysis is progressively more antero-dorsal in position on the side of the prezygapophysis. The angle which the diapophysis makes with the vertical in the transverse plane varies from 140 degrees in the third vertebra to 155 degrees in the fifth and then to 80 degrees in the ninth. The postzygapophysis of the third vertebra is quite slender with a well-developed dorsal ridge but distally it is flatter and broader. The remaining postzygapophyses are wider and thicker so that the dorsal ridge becomes progressively less conspicuous. Distally the postzygapophyses are broader and flatter but the separation of this region is less well marked. On this distal part in cervical vertebrae 6 and 7 there are well developed and irregular surface markings.

In cervical vertebrae 3 and 4 the neural spine was probably only a slight ridge; in 5 and 7 it is small and thick with a triangular lateral outline while in 8 and 9 it is much larger, forming a thin triangular sheet. In cervical vertebrae 3 and 4 the pre- and postzygapophyses form a continuous curve with the neural arch (Text-fig. 20B). In the fifth there is a distinct excavation of the wall of the neural arch and the line of the postzygapophysis continues antero-medially to the end of the neural spine. In cervical vertebrae 6, 7 and 9 this lateral space between the pre- and postzygapophyses becomes slightly deeper anteriorly and slightly wider. However, in cervical 8 this space forms a narrow cleft as the body of the neural arch is considerably enlarged. On the flat area so formed are well-developed insertion markings which are adjacent to those on the postzygapophyses of the preceding vertebra.

The third rib, like those of the remaining cervicals, is double-headed. The tuberculum is longer and wider than the capitulum. This rib lacks the anteriorly directed spine present on the fourth rib (Text-fig. 19). The ribs of cervicals 4 to 9 show a number of progressive trends as illustrated (Text-figs. 19, 20). The capitulum becomes longer, the anteriorly directed spine is reduced and the ribs become longer and wider so that they are more sheet-like. In the seventh to ninth ribs the lateral surface is convex, the medial surface concave, the anterior edge thick and rounded and the posterior part thin and sharp-edged. In the eighth and ninth ribs there is a non-articular extension of the capitulum on its medial side.

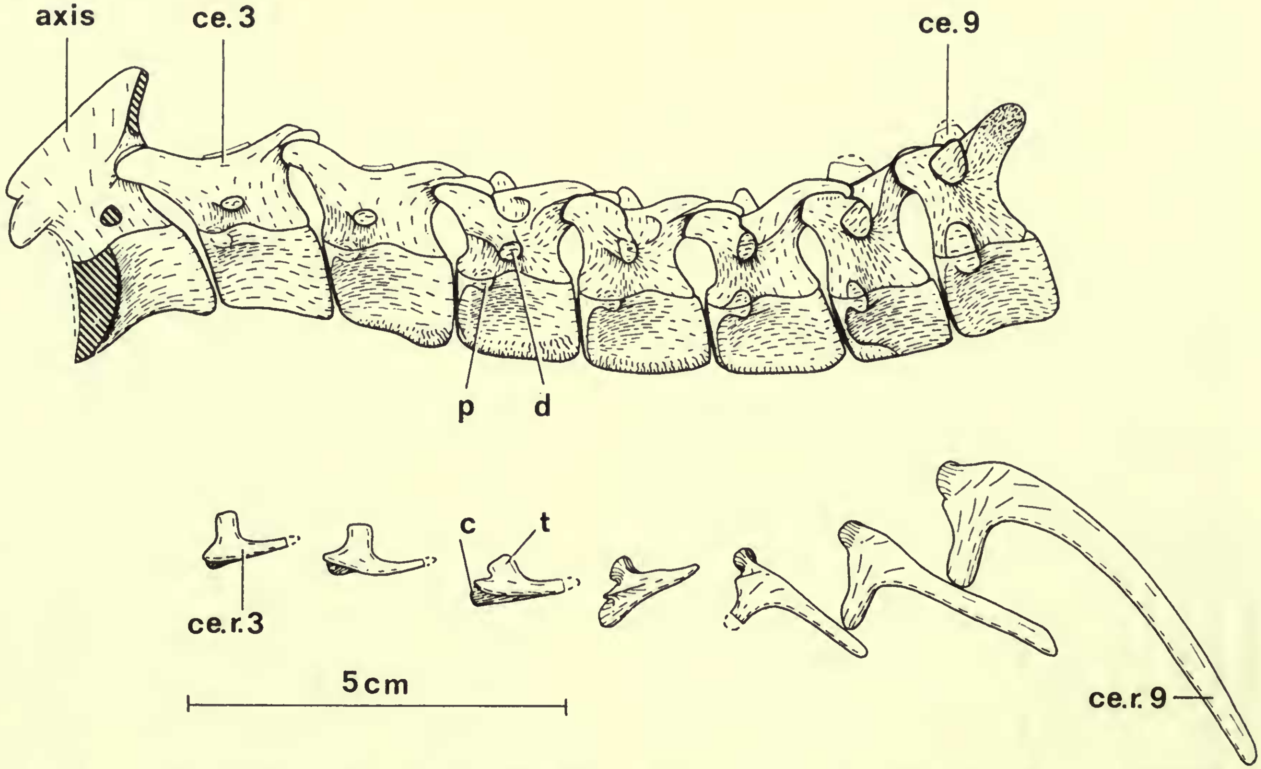


FIG. 19. *Hypsilophodon foxii.* Cervical vertebrae 2 to 9 of R196, ×1. Lateral view with ribs displaced. Abbreviations: c, capitulum; ce., cervical vertebra; ce.r., cervical rib; d, diapophysis; p, parapophysis.

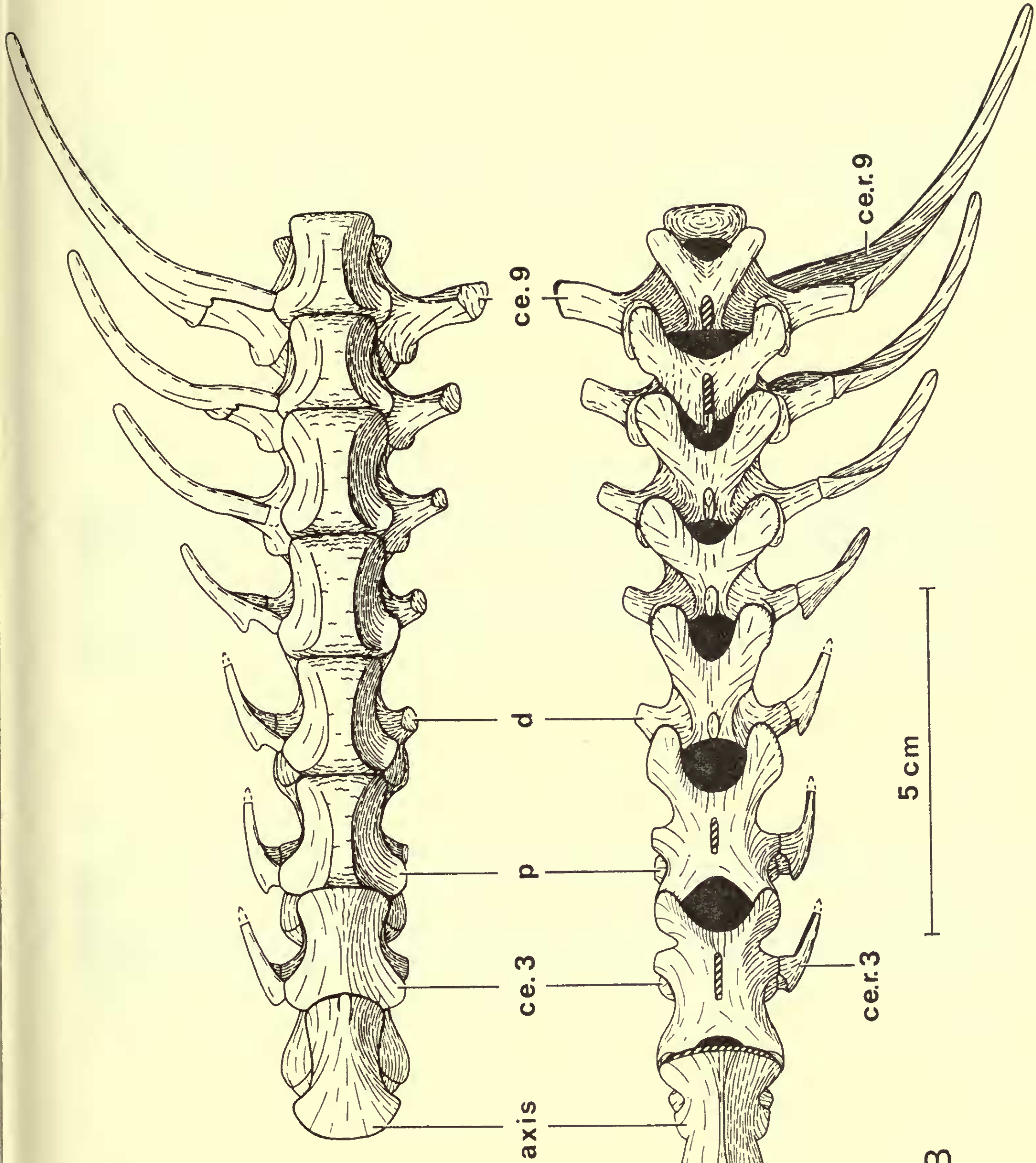


FIG. 20. *Hypsilophodon foxii.* Cervical vertebrae 2 to 9 of R196 with ribs in position, × 1. A, ventral view; B, dorsal view. Abbreviations as in Text-fig. 19.

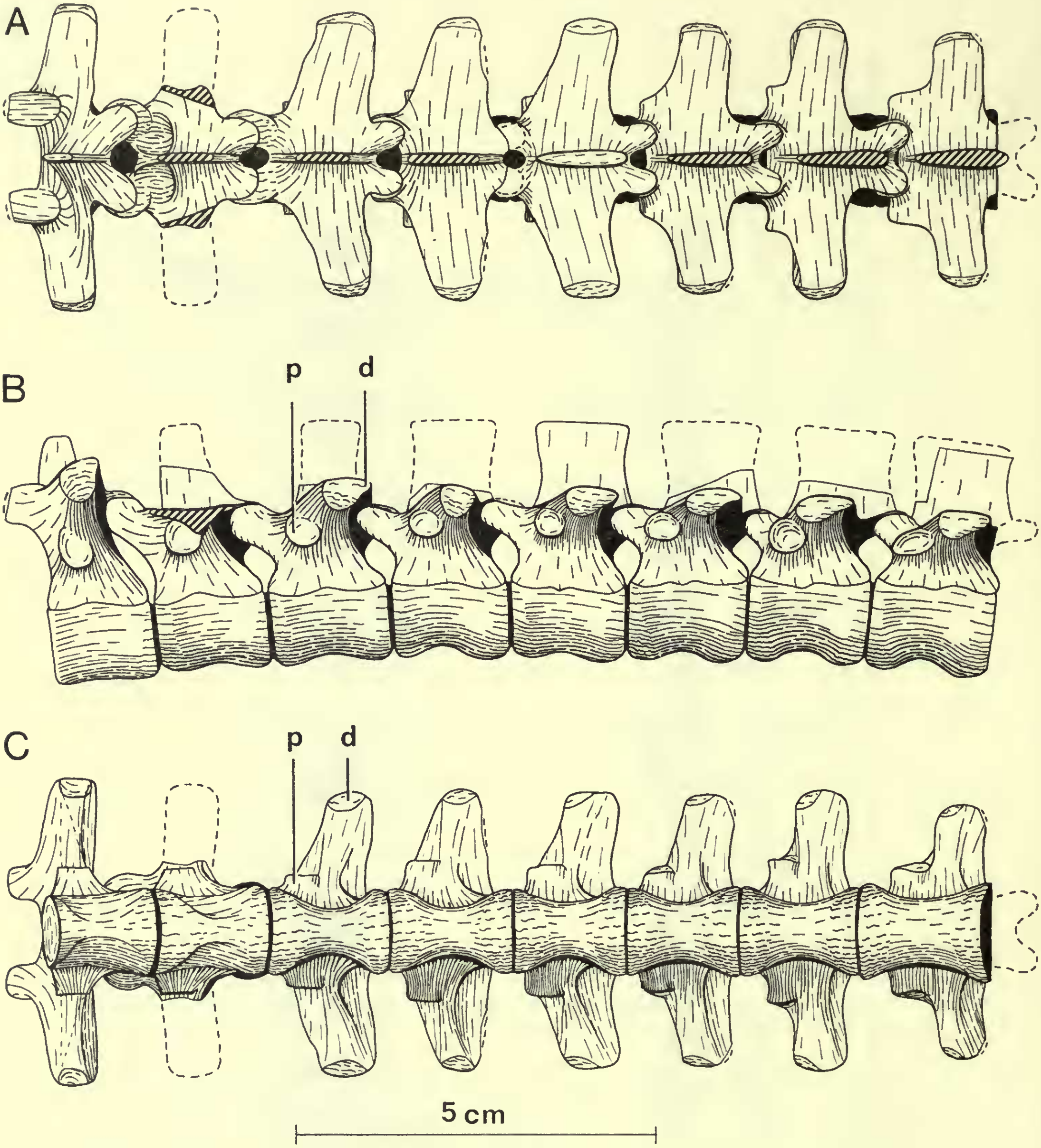


FIG. 21. *Hypsilophodon foxii*. Dorsal vertebrae 1 to 8 of R196, × 1. A, dorsal view; B, lateral view; C, ventral view. Abbreviations: d, diapophysis; p, parapophysis.

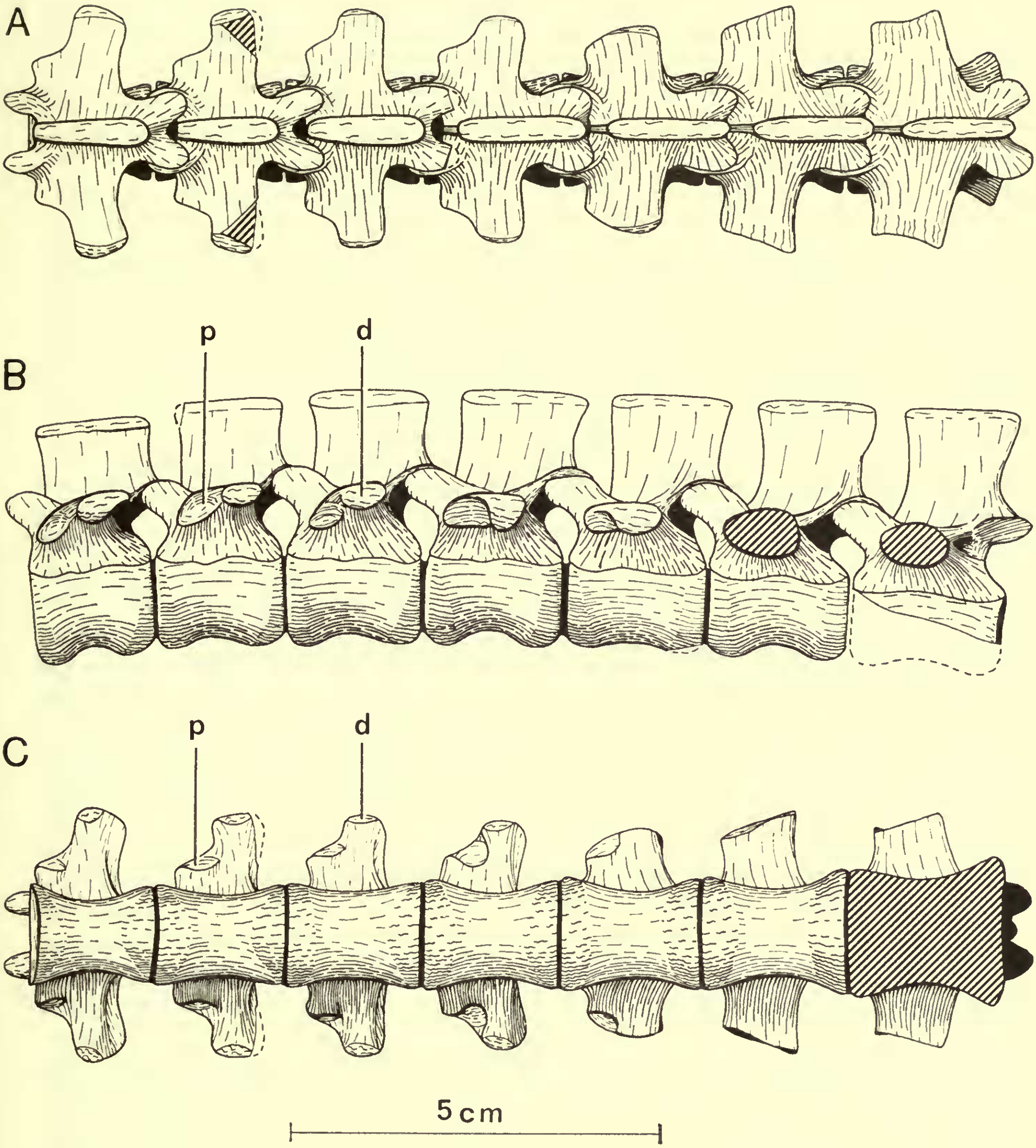


FIG. 22. *Hypsilophodon foxii.* Dorsal vertebrae 9 to 15 of R196 (supplementary details from R2477a), × 1. Views and abbreviations as in Text-fig. 21.

iii) DORSAL VERTEBRAE (Text-figs. 21, 22)

All the centra are amphicoelous. The posterior face of the last dorsal vertebra has two lateral concave areas separated by a dorso-medial ridge. The length of the centrum increases slightly with each successive vertebra. In the first dorsal the middle part of the centrum is laterally compressed so that a thin ventral edge is formed (Text-fig. 21C). The degree of compression decreases posteriorly, so that this ventral part becomes thicker and more rounded. The thicker anterior and posterior regions of the centra are covered with muscle insertion markings which are especially strong ventrally.

The diapophysis remains at about the same height on the neural arch throughout the series (Text-figs. 20B, 21B). The level of the parapophysis drops quite sharply from dorsals 1 to 4 but behind this there is only a very slight drop. The diapophysis and parapophysis become progressively closer together and are united in the last two dorsal vertebrae. In the first dorsal the prezygapophyses are large and wide apart but in the next five vertebrae they become progressively smaller and closer together (Text-fig. 20A). Posteriorly the prezygapophyses become slightly longer and the level varies as shown in Text-fig. 21B. The articular surfaces of all the prezygapophyses make an angle of about 45 degrees with the horizontal.

The angle between the transverse process and the vertical varies from 60 degrees in the first dorsal to 70 degrees in dorsal 4 and 85 degrees in dorsal 8, the processes being more or less horizontal in the remainder. The bases of the transverse processes of the first five dorsal vertebrae become more ventral (Text-fig. 20B) and posterior (Text-fig. 20C) in position. The thin overhanging part at the base of the transverse process is reduced, passing posteriorly, so that more of the diapophysis becomes visible in dorsal view (Text-fig. 20A). In the sixth dorsal the dorsal edges of the diapophysis and the transverse process form a continuous curve. Posteriorly at its base the transverse process forms a flattened sheet which continues as the postzygapophysis. This sheet is small in the first dorsal but considerably larger in the second; it is then progressively reduced and is absent in the fourteenth and fifteenth dorsals. The first neural spine is thin, the fifth is thicker and larger (Text-fig. 20A, B) while the last seven dorsals have a well-developed thickening dorsally so that a thick edge is formed (Text-fig. 21B).

All except the last one or two dorsal ribs are double-headed. Anteriorly the thoracic ribs are curved, especially near their upper ends, with a superficially flattened and broad distal part. Posterior to the seventh dorsal vertebra the ribs become progressively shorter, straighter and the lateral expansion is lost. The capitulum is borne on the proximal end of the rib while the tuberculum is on a more dorsolaterally placed step and faces dorso-medially. On the anterior ribs the tuberculum is widely separated from the capitulum but more posteriorly the two heads are progressively closer together; thus they are scarcely distinguishable on dorsal rib 14 while rib 15 is single-headed. These last two ribs are fused with the end of the transverse process.

The sternal segments of the dorsal ribs are always present but are not always ossified. In R196 the sternal segments of the first three dorsal ribs and part of the fourth (Text-fig. 37E) are preserved on the left side together with parts of the first three of the right side (Text-fig. 37B). The first three segments contact the thick and roughened dorso-lateral edge of the sternum while the fourth contacts the distal part of the third (Text-fig. 37E). Distally the first three segments become dorso-ventrally flattened and thicker. In *Parksosaurus* the first six dorsal ribs have sternal segments (Parks 1926) and this may have been the case in *Hypsilophodon.*

iv) SACRAL VERTEBRAE

There are two distinct types of sacrum found in *Hypsilophodon* ; the significance of this dimorphism will be discussed below (p. 122).

The sacrum of R196 (Text-fig. 23) consists of six coossified centra. But the ribs of the first vertebra are borne on the transverse processes and do not contact the ilium (Text-figs. 23, 25C) ; there are only five pairs of sacral ribs, which belong to vertebrae 2–6. This is the *pentapleural* condition. Therefore, strictly speaking, the 'first sacral' vertebra is a dorsal ; R196 has 16 dorsal vertebrae and 5 true sacrals. Functionally, however, this last dorsal vertebra is an integral part of the sacrum because the expanded posterior part of its massive centrum has an extensive sutural contact with the first true sacral ribs (i.e. the ribs of the second vertebra, Text-figs. 23, 25E).

The sacra of *Parksosaurus, Thescelosaurus* and *Dysalotosaurus* are very similar to this. In his description Parks (1926) – followed by Sternberg (1940) and Janensch (1955) – numbered the massive dorso-sacral vertebra as S1 and the other five vertebrae as S2–S6 ; yet, oddly enough, the five pairs of sacral ribs borne by those five vertebrae were numbered 1–5. Thus the second vertebra bears the first rib, the third vertebra the second rib and so on down the series. Confusing though this may seem, for the sake of consistency the same system of numbering will be applied to the pentapleural sacrum of *Hypsilophodon.*

By contrast, in R193 and R195 the first vertebra (Text-figs. 24, 25B, 27) *is* a true sacral because its ribs suture with the centrum and neural arch and contact the pubic peduncles of the ilia ; thus the sacrum in these individuals has 6 pairs of sacral ribs. This is the *hexapleural* condition, with only 15 dorsal vertebrae but with 6 sacrals. Because the ribs of sacral vertebrae 2–6 (numbered 1–5) are obviously homologous to the 5 true sacral ribs of R196 and to those of other lower ornithopods, Parks' system of numbering will be applied also to the hexapleural sacrum of *Hypsilophodon,* with the second vertebra bearing the *first* rib and so on. The problem then arises : how should the rib borne by the first sacral vertebra be numbered in hexapleural individuals? The solution adopted, is to call it the 'new sacral rib' (Text-figs. 24, 25B, 27 ; see Section vi). Though this too may be confusing, it seems likely that worse confusion would result from a complete renumbering.

In R196 the anterior end of the first centrum is transversely expanded (Text-fig. 23C) and its face is markedly concave (Text-fig. 25C). The slightly expanded posterior surface of centrum 6 is very gently concave (Text-fig. 26D). Each zygapophysis makes about a right angle with the other but they are closer together posteriorly. The postzygapophyses of sacrals 1 to 5 fit into a square space formed by the anterior edge of the neural arch and the prezygapophyses of the next vertebra. In sacral 1 the

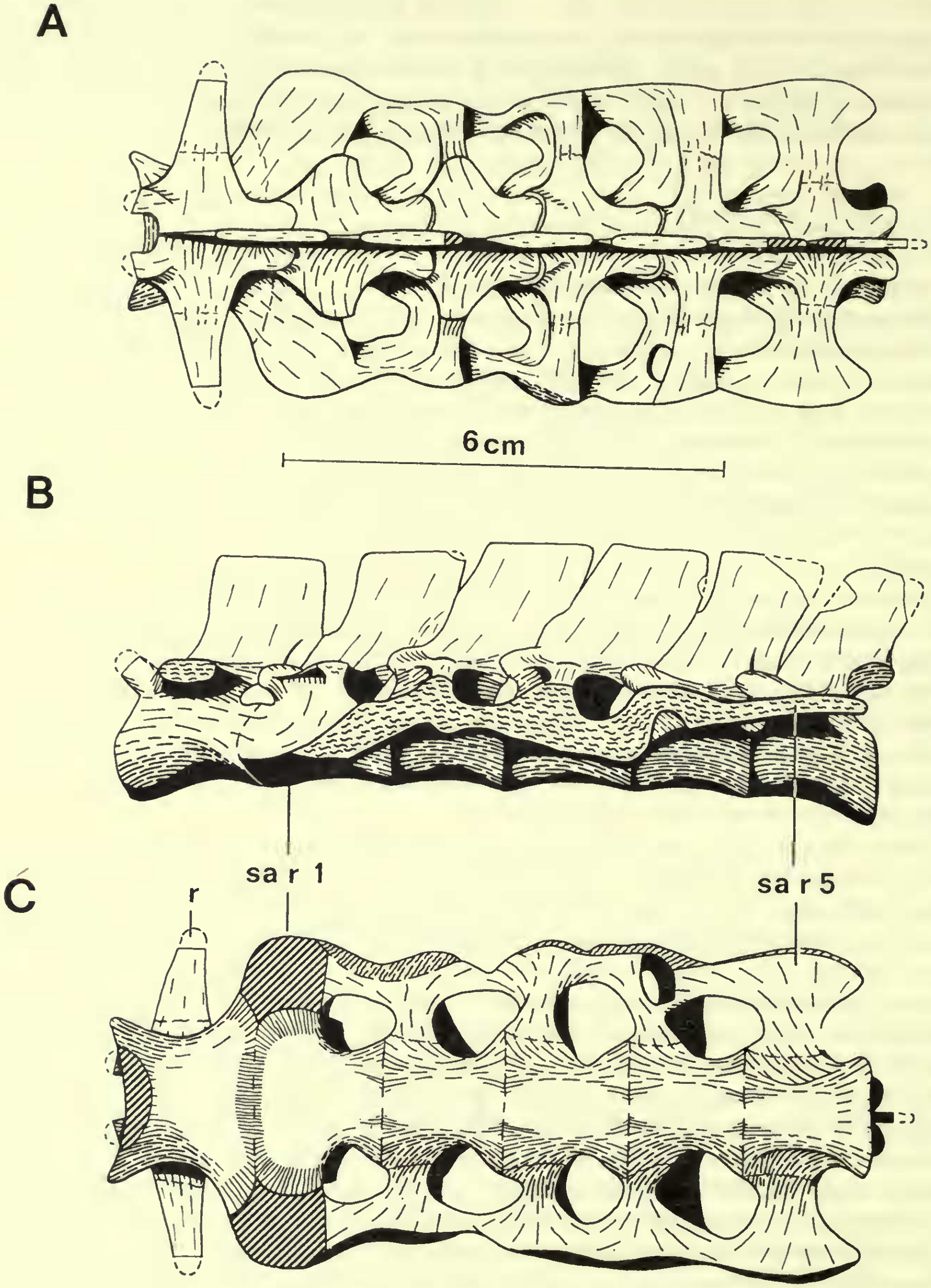


FIG. 23. *Hypsilophodon foxii*. Sacrum of R196 – pentapleural type, × 1. A, dorsal view; B, lateral view; C, ventral view. Abbreviations: r, rib of first sacral vertebra (dorsosacral); sa, sacral vertebra; sa r, sacral rib.

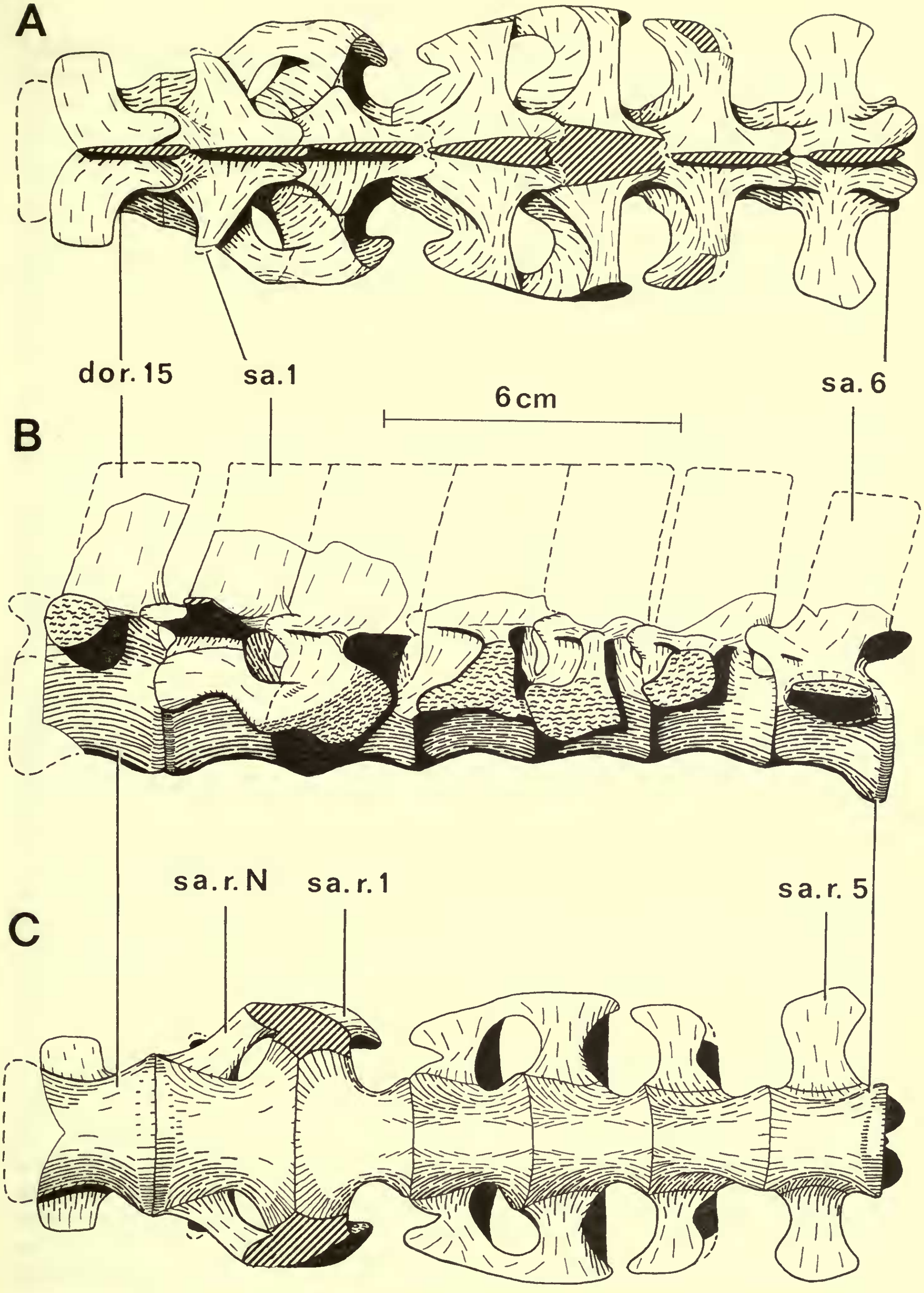


Fig. 24. *Hypsilophodon foxii*. Last dorsal vertebra and sacrum of R193 – hexapleural type, × ¾. A, dorsal view, B, lateral view; C, ventral view. Abbreviations: dor, dorsal vertebra; sa, sacral vertebra; sa r, sacral rib; sa r N, new sacral rib.

transverse process is large and bears a free rib on its distal end. In the remaining sacral vertebrae the transverse process is sutured ventrally and also (except in sacral 2) laterally to a sacral rib. The angle between the distal part of the transverse process and the vertical varies, being 70 degrees in sacral 1, 90 degrees in sacral 4 and 100 degrees in sacral 6. In sacral vertebrae 1 and 6 the sides of the neural arch are excavated so that the anterior end of the base of the neural spine is thin. Posteriorly there is a slight increase in thickness from sacral 1 to 3, then a decrease to sacral 6. The lower half of each neural spine is thin anteriorly and posteriorly so that the edges of adjacent spines touch. The anterior thin sheet is especially large in sacrals 5 and 6 while the posterior thin sheet, which is developed between and above the postzygapophyses, is largest in sacral 5 but absent in sacral 6.

v) SACRAL RIBS

The central sutures are not clearly visible in R196 (Text-fig. 23) but can be seen in the four sacral vertebrae of R195, in which the different parts have been dissociated (Text-figs. 25B, E, F, 26A, 27 ; for sac. r. N see Section vi), and in R193 (Text-figs. 24, 26B, C). Each sacral rib projects not from the middle of the centrum, but more anteriorly, so that its anterior edge is borne by the centrum of the preceding vertebra. The base of each rib contacts the lower surface of the transverse process and it is sunk into the side of the neural arch. The flat ventral surface of the first sacral rib is level with the ventral surface of the centrum (Text-fig. 23B). Proximally the bases of the remaining sacral ribs are high on the centrum, with the second slightly higher than the others.

In R196 the dorsal parts of the sacral ribs vary (Text-figs. 23A, B). In the first sacral rib the dorsal part is thin with a sharp dorsal edge. In the second and third sacral ribs it is still thin, but its dorsal edge is thicker and is attached to the end of the transverse process. In the fourth sacral rib all the dorsal part is thicker and postero-dorsally inclined. There is a progressive dorso-ventral flattening of the more distal part of sacral ribs 3, 4 and 5 (Text-fig. 23B) so that the fifth rib (Text-fig. 26D) is practically horizontal and the thickened dorsal edge has merged with the rest of the rib. On the dorsal surface of the ribs and transverse processes there are well-developed markings across the line of suture. These are absent on the second sacral vertebra, the transverse process of which does not contact a sacral rib at its lateral end ; consequently the muscles concerned presumably attached to the end of this process.

vi) THE HEXAPLEURAL TYPE OF SACRUM

In specimens of this type (R193, R195, R2477a, R5829, R5830) the rib of the first sacral vertebra is no longer a free dorsal rib, but has become a sacral rib ; this vertebra is therefore a true sacral rather than a dorso-sacral vertebra. The rib is no longer attached to the transverse process, but is borne ventrally and sunk into the side of the centrum and neural arch (Text-figs. 24, 25B, D, 27). The rib base is enlarged antero-posteriorly and is partially borne by the centrum of the preceding vertebra (Text-figs. 24B, 25B, D, 27B). Thus, in comparison with the pentapleural type with five sacral ribs (Text-fig. 23; R2477b, R8422), there is an additional sacral rib which is termed the 'new sacral rib' (see above). This rib has a constricted shaft beyond which it is slightly expanded and meets an anterior projection from the proximal end of the first sacral rib. The distal face of this new rib forms a smooth and slightly concave surface (shown in R195, right rib).

The new position of the rib of the first sacral vertebra has resulted in a few differences in the form of the vertebra when compared with that of the first sacral (dorso-sacral) of the pentapleural type described above. The transverse process, because it no longer bears the rib, is very thin dorso-ventrally. In anterior view (Text-figs. 25B, D) it tapers to a point and there is no distal facet. There are no well-developed muscle scars on the distal part of the dorsal surface as the muscles concerned inserted on the lateral end of the process. Anteriorly the sides of the neural arch and the centrum are recessed for the new sacral rib.

The sacrum of R5829 differs somewhat from the other hexapleural sacra. The new sacral rib is rather damaged but it was certainly sutured to the side of the first sacral centrum and neural arch. Dorsally the right transverse process of the first sacral vertebra bears well-developed muscle scars. These insertion markings are found only when a rib is present and they run across the line of suture between the rib and the transverse process. Because these markings are complete the proximal part of the new sacral rib is still attached to the end of the transverse process (the rest of the rib is lost). Consequently the new sacral rib in R5829 has the same connections with its vertebra as do the other sacral ribs. The first sacral rib (i.e. the rib of the second sacral vertebra) bears an anteriorly directed process that would have met the new sacral rib. However, the dorsal edge of the first sacral rib is thickened; it is sutured to the end of the transverse process and there are muscle striations running across the line of suture. This is in contrast to all other sacra, pentapleural or hexapleural, in which this rib has a sharp dorsal edge and there is no contact with the distal end of the transverse process.

vii) OTHER VARIATIONS IN THE SACRUM

The degree of contact between the neural spines of the sacral vertebrae varies (Text-figs. 23B, 24B, 27B). In R193 and R196 the part of the spine adjacent to the contact edge consists of a thin sheet. In R195 and R2477a the whole of the neural spine is thick with well-developed sutural ridges along the contact edge (Text-fig. 25E). In addition there is a small sutural contact between the neural spine bases of the fifteenth dorsal vertebra and the first sacral vertebra (Text-fig. 25B). This contact is also present in R5829 but there are no comparable sheets between the zygapophyses of the other specimens. The degree of fusion of the neural spines is an individual variation because it is not related to the size of the specimens (see list below). The ankylosis of the neural arch and the centrum of the sacral vertebrae appears to be an age variation. The length of the first three centra of the sacrum is the best index of size available. The neural arch and centrum are separate (as are the individual centra) in R5830 (38 mm), and R195 (51 mm) but they are all ankylosed in R2477a (± 50 mm), R2477b (54 mm), R196 (55 mm), R5829 (± 67 mm),

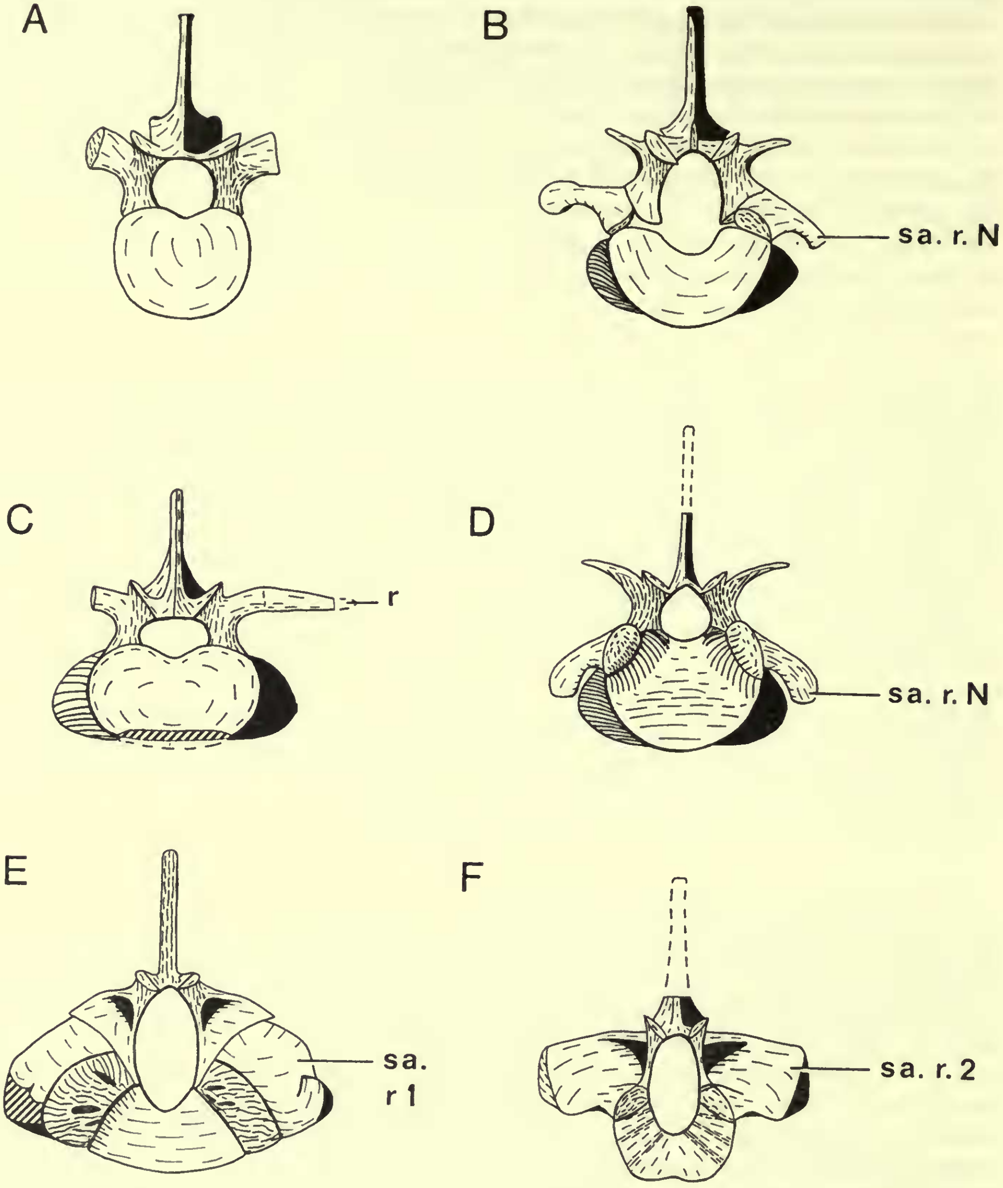


FIG. 25. *Hypsilophodon foxii.* Anterior view of vertebrae. Dorsal vertebra: A, fifteenth of R195, × 1. Sacral vertebrae: B, first of R195, × 1; C, first of R196 (dorso-sacral), × 1; D, first of R193, × $\frac{2}{3}$; E, second of R195, × 1; F, third of R193, × $\frac{2}{3}$. Abbreviations: r, rib of first sacral vertebra; sa r, sacral rib; sa r N, new sacral rib.

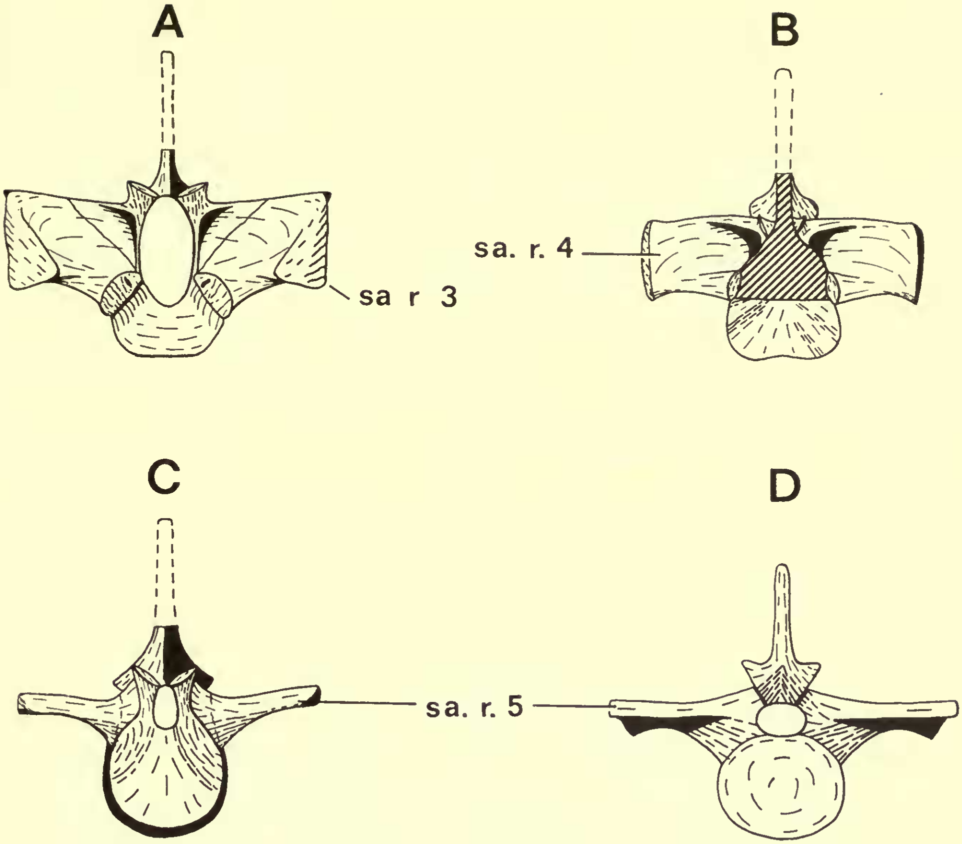


Fig. 26. *Hypsilophodon foxii.* Anterior view of sacral vertebrae. A, fourth of R193, × $\frac{2}{3}$; B, fifth of R193, × $\frac{2}{3}$; C, sixth of R193, × $\frac{2}{3}$; D, posterior view of sixth of R196, × 1. Abbreviations: sa r, sacral rib.

R8422 (71 mm) and R193 (75 mm). The anterior face of the centrum of the first sacral varies; it is transversely concave in R196 (Text-figs. 23C, 25C), almost flat in R195 (Text-figs. 25B, 27C) while in R193 (Text-figs. 24C, 25D) the medial part is flat with deep dorso-lateral depressions in the region of the new sacral rib. The ventral surface of the first two centra varies: the medial part of the first of R196 (Text-fig. 23C) is rather flat while in R193 (Text-fig. 24C) and R195 (Text-fig. 27C) it is transversely convex and longitudinally concave; that of the second is transversely concave in R195 and R196 but convex in R193.

viii) CAUDAL VERTEBRAE AND CHEVRONS

In the small individual R196 the first 19 caudals are present while in the larger individual R196a there are 29 from the posterior part of the tail. The first vertebra without a transverse process is the eighteenth caudal of R196 and the ninth preserved

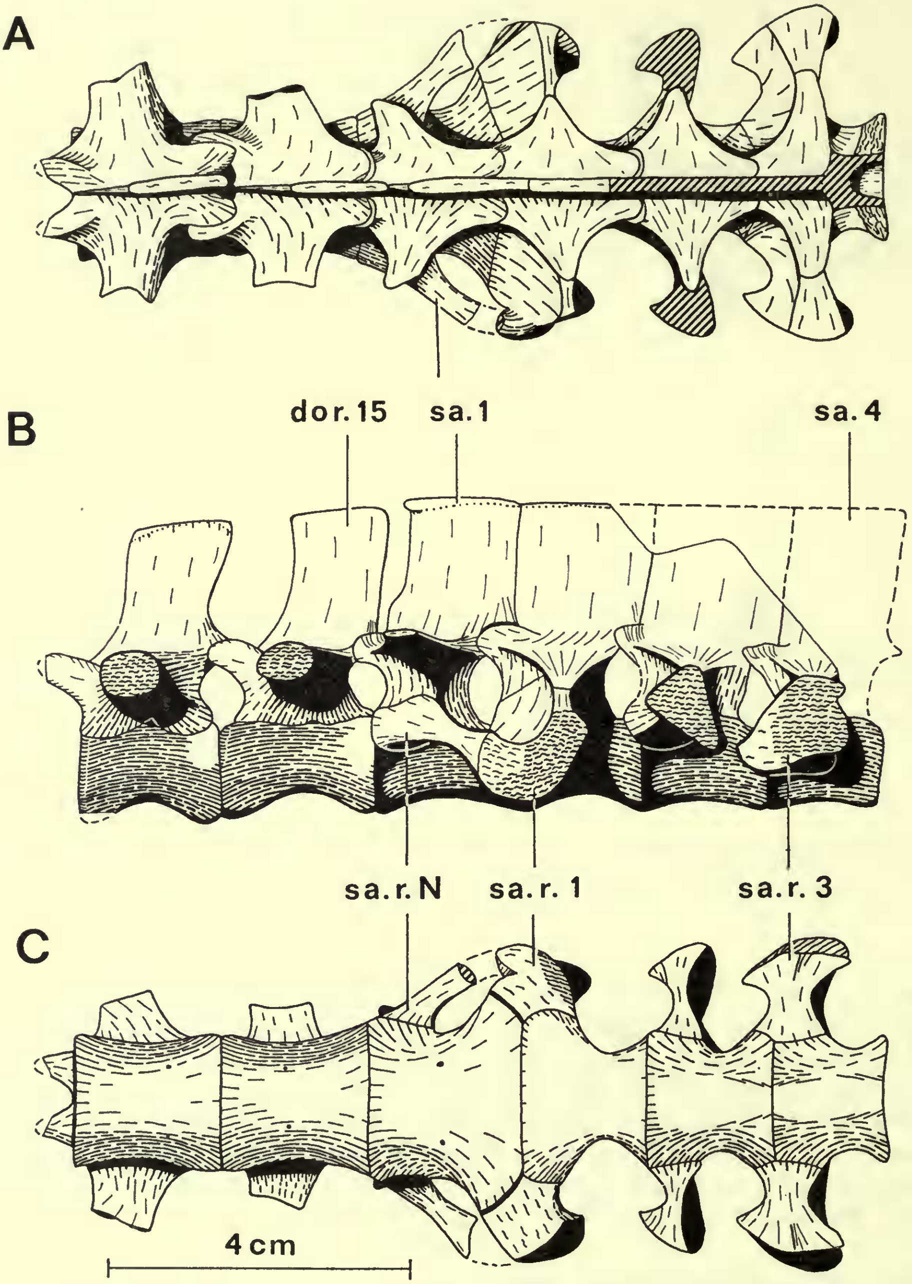


Fig. 27. *Hypsilophodon foxii.* Dorsal vertebrae 14, 15 and sacral vertebrae 1 to 4 of R195, × 1. A, dorsal view; B, lateral view; C, ventral view. Abbreviations: dor, dorsal vertebra; sa, sacral vertebra; sa r, sacral rib; sa r N, new sacral rib.

vertebra of R196a. This suggests that the first 9 tail vertebrae are missing in the latter series, those present being caudals 10 to 38. The most posterior caudals present are not greatly shortened. A comparison with the tail in *Thescelosaurus* (see Gilmore 1915) indicates that 10 or so vertebrae are probably missing from the distal end of the tail of the larger specimen.

The first caudal centrum is opisthocoelous but the remaining centra are amphicoelous. Throughout the series the centra become progressively lower and thinner. Posterior to the eighteenth caudal the lateral and ventral surfaces become flatter so that the ventral edge is square in section. In addition there is a square dorsal outline above. All the transverse processes point slightly upwards at an angle of about 10 degrees to 15 degrees to the horizontal. The distal part is postero-ventrally directed only in the first caudal (Text-figs. 28A, C, 30A, C). Some of the variation in the horizontal plane (Text-figs. 29, 31) is due to distortion. The transverse process of the seventeenth caudal is represented by a very slight bump with no trace at all on the eighteenth.

In the first 12 caudal vertebrae the articular surfaces of the zygapophyses become progressively smaller, more vertical and closer together but then remain constant in the remaining caudals preserved. In lateral view (Text-fig. 28A) the prezygapophyses become thinner but the length remains about the same. However, internally the space at the base of the prezygapophyses is filled in with bone. By caudal 12 the postzygapophyses have become round vertical plates close together on the edge of the neural spine. They are embraced by the correspondingly small prezygapophyses.

The main body of the neural arch becomes progressively lower and thinner along the series. The neural spine of the first caudal is slightly taller and narrower than in the last sacral vertebra. The thin anterior part is less extensive but the part of the spine dorsal to the postzygapophyses is thicker. The anterior thin part is progressively reduced in the first six caudals so that the neural spine is slightly shorter ventrally (Text-fig. 28A). Posterior to the ninth caudal the neural spines become progressively lower but the ventral part becomes wider. The neural spines seem to disappear at about the thirty-sixth caudal in R196a.

The first chevron is borne between the centra of the first two caudals and was found in place in R196 (Text-fig. 28A). In R193 this region had already been prepared but a chevron was originally present because these two centra have the same facets (Text-fig. 30A). Hulke (1882 : 1046) stated that the second caudal has 'a single facet, the first chevron being articulated with the second and third caudal vertebrae'. However, the condition of the second centrum cannot be determined from his figure (Hulke 1882, pl. 74, fig. 9) and this specimen cannot be found. The first chevron is a small nubbin of bone that is slightly flattened dorso-ventrally (Text-fig. 28A). The ventral part is damaged and there may have been bone enclosing the haemal artery. The second chevron appears to be flattened antero-posteriorly while the third is circular in cross-section and tapers distally (Text-figs. 28A, B). In the fourth and successive chevrons the distal part becomes longitudinally expanded and flat while the proximal part becomes narrower with the formation of a short shaft region. In all the chevrons the articular surface for the preceding centrum is slightly smaller than that for the posterior one.

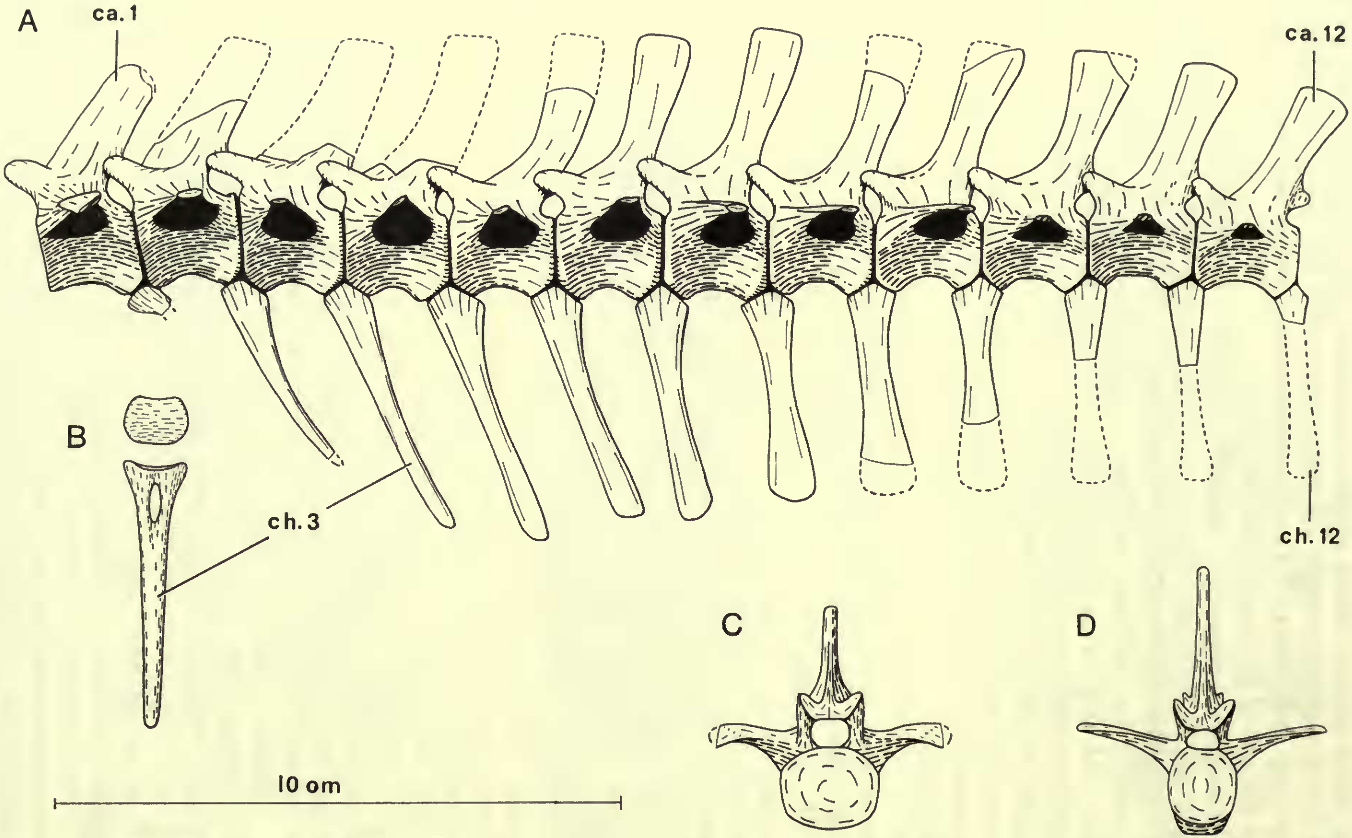


FIG. 28. *Hypsilophodon foxii.* Caudal vertebrae R196, × $\frac{3}{4}$. A, lateral view caudals 1–12 with chevrons; B, dorsal and anterior views of chevron 3; C, anterior view of caudal vertebra 1; D, anterior view of caudal vertebra 6. Abbreviations: ca, caudal vertebra; ch, chevron.

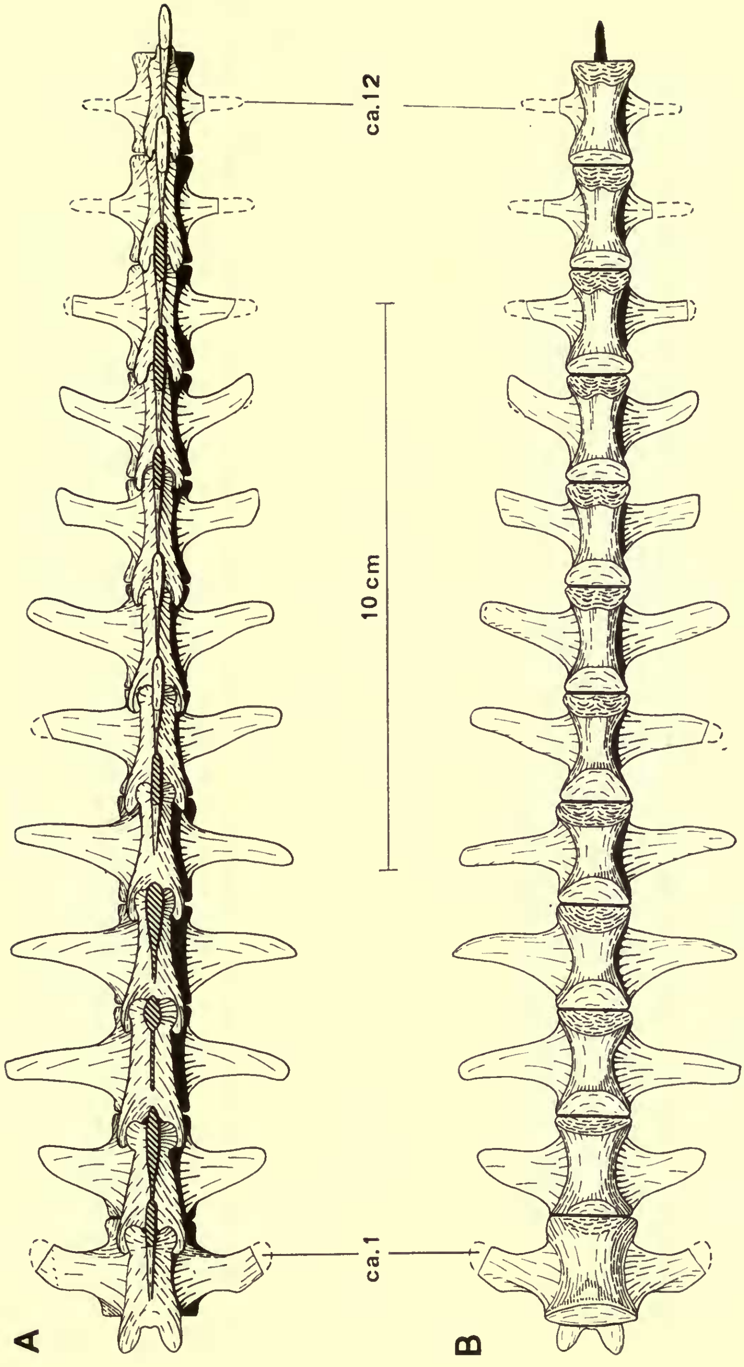


Fig. 29. *Hypsilophodon foxii.* Caudal vertebra 1–12 of R196, × ¾. A, dorsal view; B, ventral view. Abbreviation: ca, caudal vertebra.

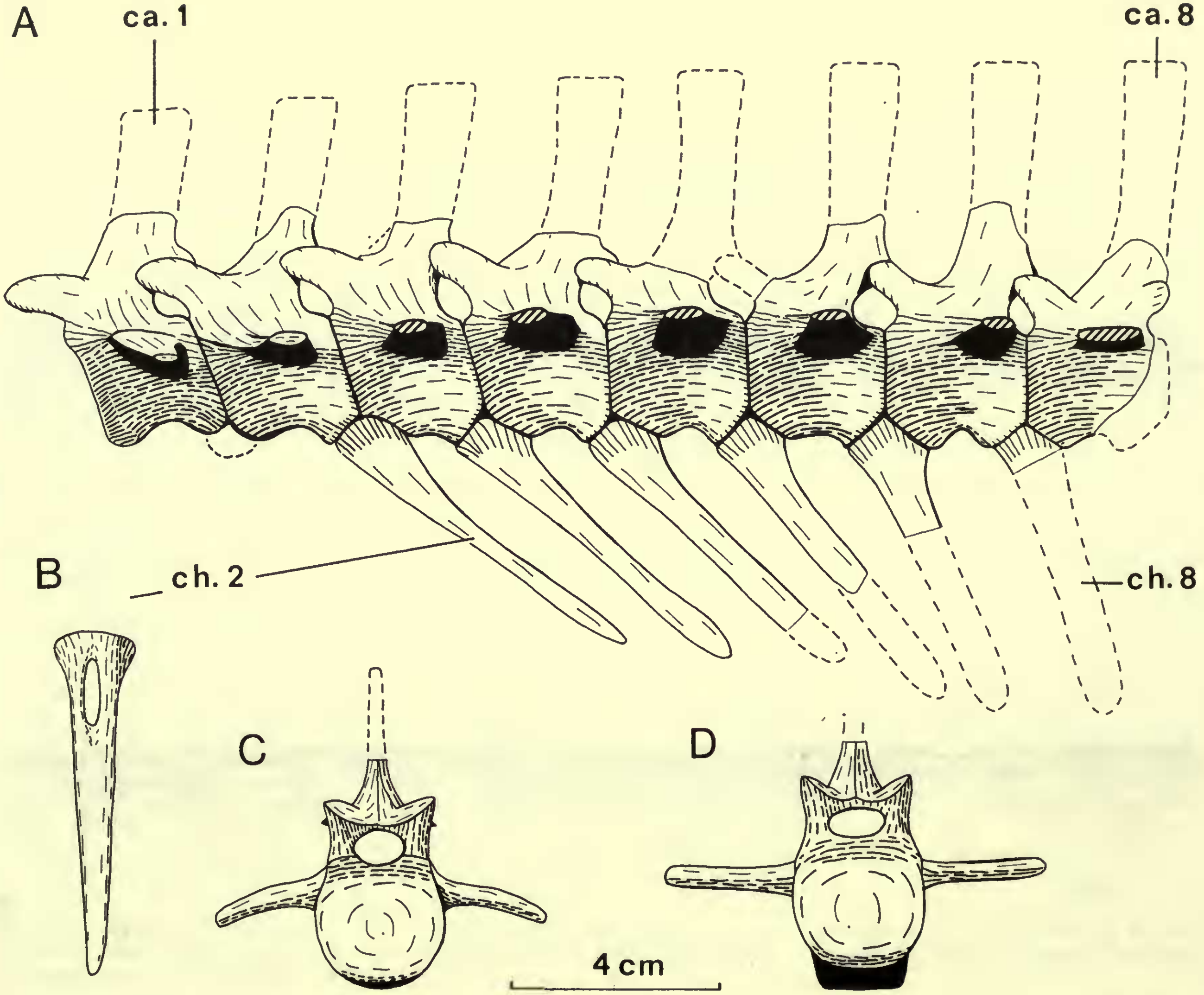


FIG. 30. *Hypsilophodon foxii*. Caudal vertebrae R193, × $\frac{3}{4}$. A, lateral view of caudals 1–8 with chevrons; B, anterior view of chevron 2; C, anterior view of caudal vertebra 1; D, anterior view of caudal vertebra 2. Abbreviations: ca, caudal vertebra; ch., chevron.

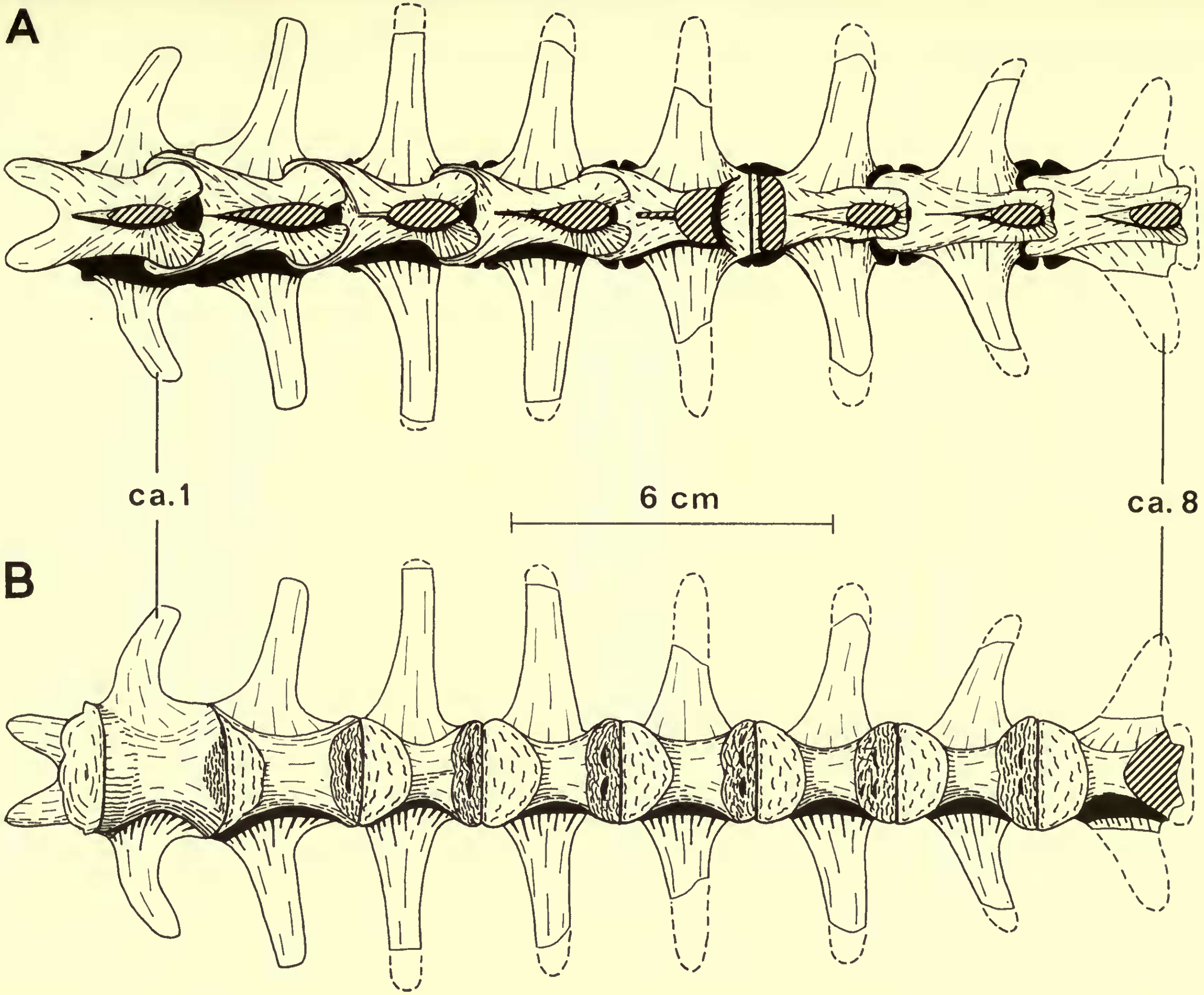


FIG. 31. *Hypsilophodon foxii*. Caudal vertebrae 1–8 of R193, × ¾. A, dorsal view ; B, ventral view. Abbreviation : ca., caudal vertebra.

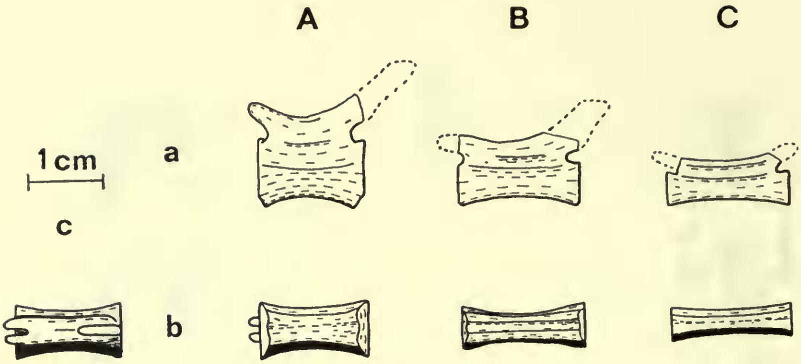


FIG. 32. *Hypsilophodon foxii.* Caudal vertebrae of R5830, × 1. A, about the twenty-fourth; B, about the twenty-eighth; C, about the thirty-seventh; a, lateral view, b, ventral view; c, dorsal view.

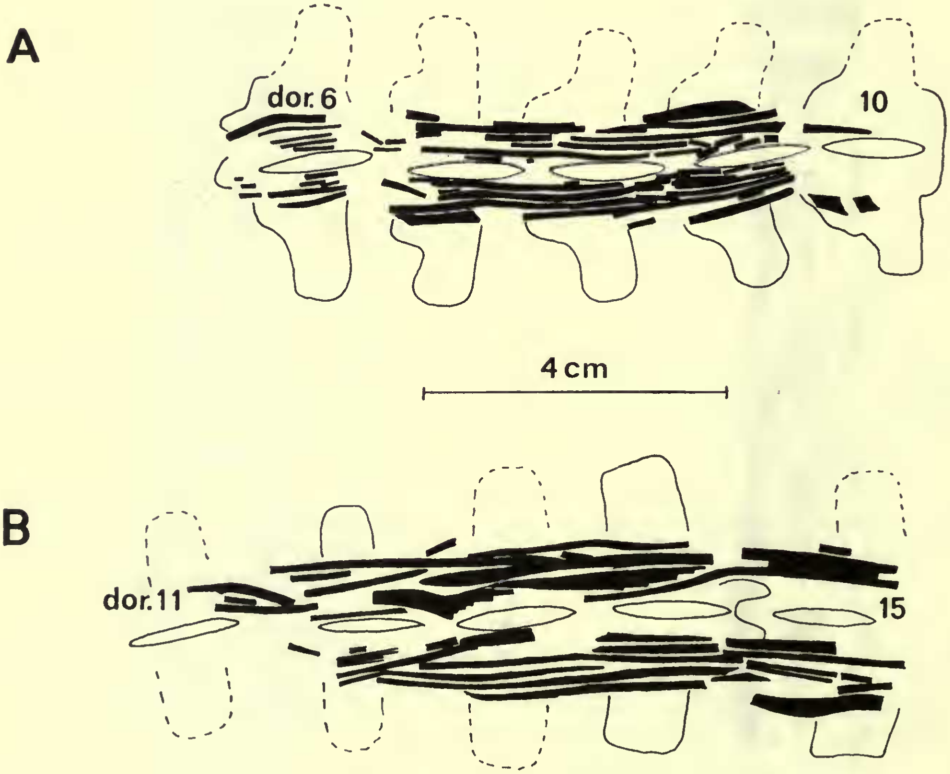
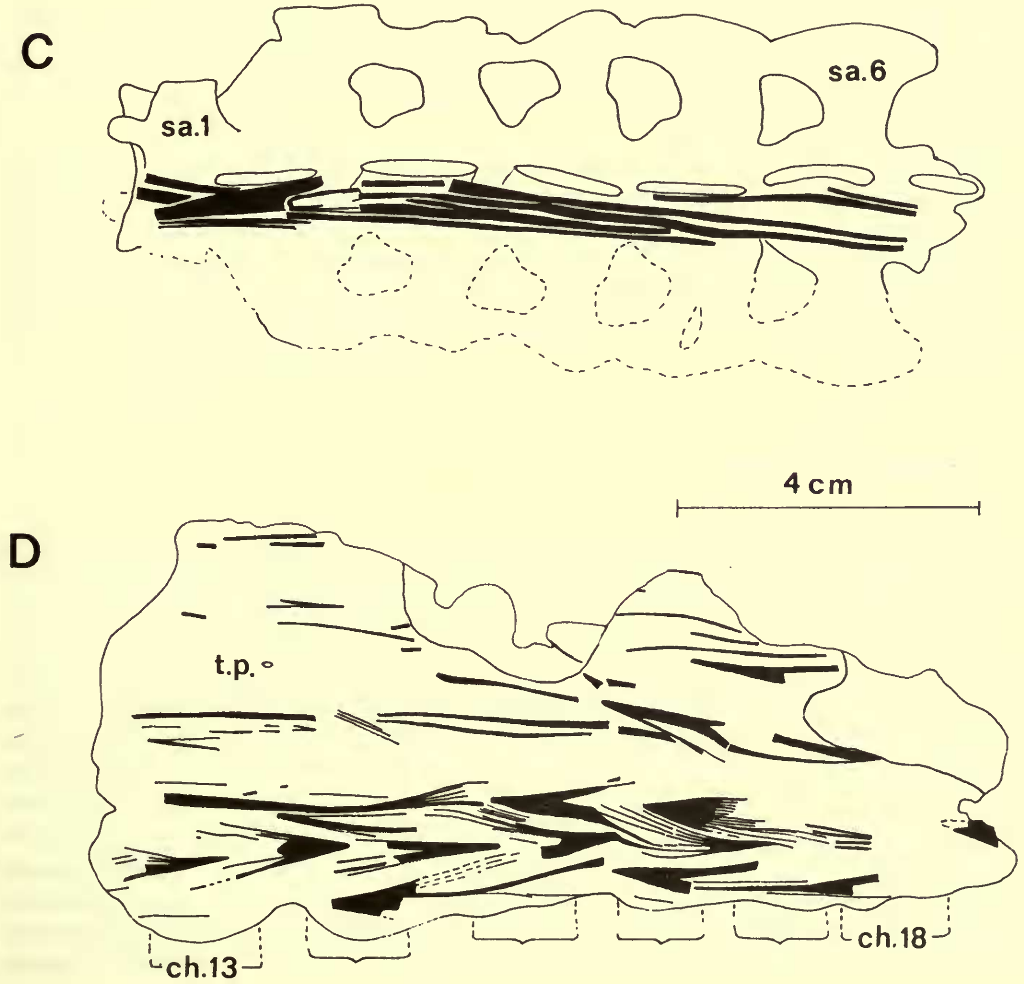


FIG. 33. *Hypsilophodon foxii.* Ossified tendons of R196, × 1. A, dorsal vertebrae 6–10 in dorsal view; B, dorsal vertebrae 11–15 in dorsal view; C, sacrum in dorsal view; D, caudal vertebrae 13–18 in lateral view. Abbreviations: ch., chevron; dor., dorsal vertebra; sa., sacral vertebra: t.p., transverse process.

c) *Ossified tendons*

Anteriorly, fragments of ossified tendons remain on the fifth dorsal of R196 but no tendons were found when the third dorsal was prepared. These vertebrae were in natural articulation and the fourth dorsal vertebra probably marks the anterior limit of the ossified tendons. Most of the tendons of the dorsal and sacral series of R196 lie immediately above the neural arches. However, this may not be natural because in R195 and R2477 the tendons occurred along the sides of the neural spines. In R195 the individual tendons span at least five vertebrae, running horizontally and close to one another ; they do not show the rhomboidal arrangement present in *Iguanodon* (see Dollo 1887) and the hadrosaurs (Lull & Wright 1942, Colbert 1962). The number of tendons on one side of a vertebra varies from six to nine but originally there were probably many more.



Only a few tendons were found when the proximal part of the tail of R196 was prepared and this probably reflects the original situation. The tendons on the chevrons of caudal vertebrae 14 to 17 are well preserved (Text-fig. 33D) and each consists of a flat sheet of bone, with fine longitudinal striations, one end of which tapers to a point while the other splays out into a series of fine rays. The complete series of rays is not preserved for any single tendon but there were at least ten per tendon. Each tendon is intervertebral in position and is about the same length as one of the adjacent centra. The tendons are arranged in rows, the individual tendons of which point in the same direction (Text-fig. 33D) while adjacent rows point in the opposite direction.

The posterior third, at least, of the tail was ensheathed by a large number of ossified tendons (Text-fig. 62). On one side of the twenty-seventh caudal of R196a there are 28 tendons in a width of 23 mm. However, there are many more than this because there are others below and, in addition, quite a few appear to have been removed during preparation. The individual tendons can be followed for a length of only two centra at the most but, because they are rather damaged, they may originally have been considerably longer. The splaying of the end of the tendon into many rays is visible in several places with both anteriorly and posteriorly pointing tendons represented.

In the dorsal and sacral series of R196 (Text-figs. 33A–C) the splaying is visible in a few places. However, all of these point anteriorly with a posterior splaying. There are a few anterior ends that are different, being slightly flattened laterally with a few strongly developed ridges and an uneven surface. Individual tendons are much longer than those of the tail and for most of their length are circular in cross-section, but they have the same fine longitudinal striations as the tendons of the caudal series.

d) *Appendicular skeleton*

i) THE PECTORAL GIRDLE

Scapula. This is about the same length as the humerus, is twisted along its length and, in addition, bowed (Text-fig. 34B) so that it followed the outer contour of the rib cage. The anterior end of the base of the scapula bears a triangular facet (cl. Text-figs. 34A, 35A) with a rounded articular surface which was probably for the clavicle. In ornithischians the clavicle itself is preserved in *Protoceratops* (see Brown & Schlaikjer 1940) and psittacosaurs (Osborn 1924). The anterior edge of the scapular blade is thin and rounded as is the posterior edge, apart from the dorsal part which is sharp. The dorsal edge is thicker where it cuts across the body of the blade and it is rather bumpy. This dorsal end-surface probably carried a cartilaginous suprascapula as described in *Parksosaurus* by Parks (1926). The lateral surface of the scapula immediately behind the clavicular facet forms a well-developed depression (Text-figs. 34A, 35A). This is continued diagonally upwards as a concave surface running along the convex curve of the scapula to meet another diagonally inclined depression from the glenoid region. Ventrally the central part forms a

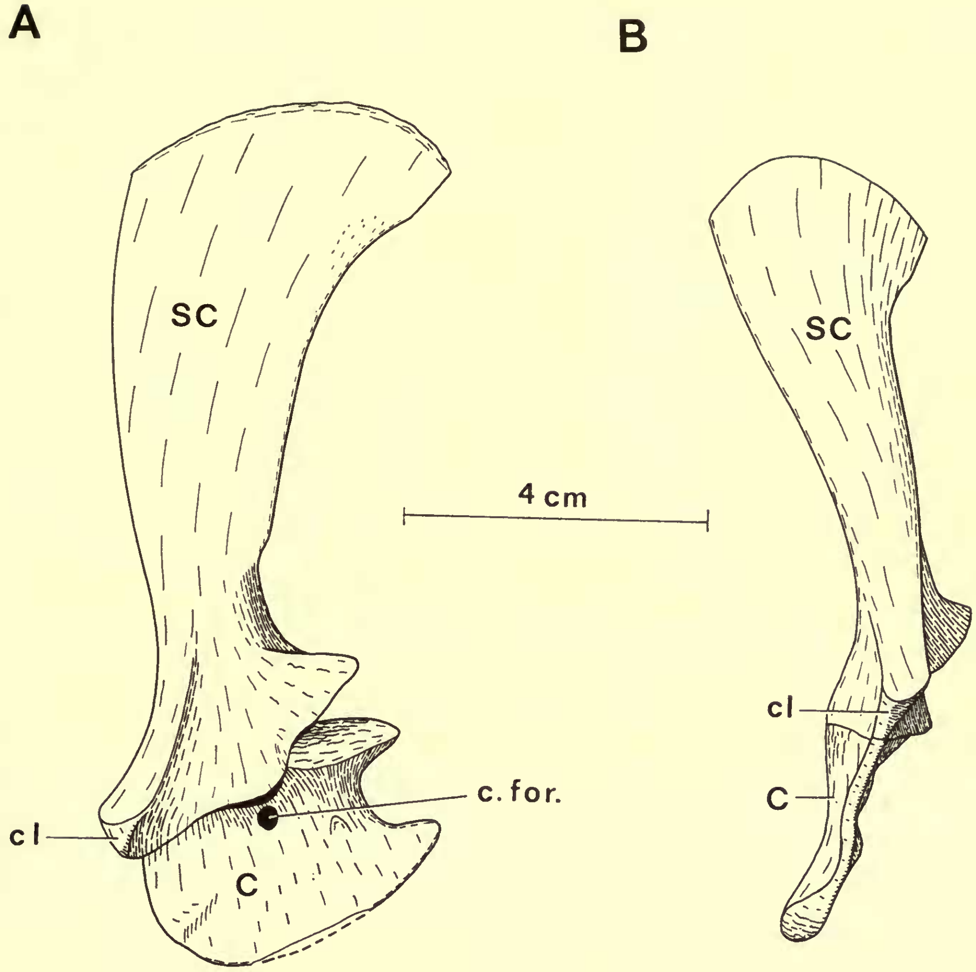


FIG. 34. *Hypsilophodon foxii*. Scapula and coracoid R196, × 1. A, lateral view; B, anterior view. Abbreviations: C, coracoid; SC., scapula; c. for., coracoid foramen; cl., facet for clavicle; gl. cav., glenoid cavity.

rounded surface that projects beyond the coracoid (Text-fig. 34). The medial surface (Text-figs. 34B, 35B) is slightly concave dorso-ventrally and convex antero-posteriorly. The ventral part forms a broad convexity which is crossed by a groove leading from the coracoid foramen (Text-fig. 35B).

The scapulae show a certain number of individual variations. Posteriorly the junction of the shaft and the blade forms a step in R196 (Text-fig. 34A) and R192 which is practically absent in R5829 and R5830 (Text-fig. 36A). The shaft is more strongly twisted in R196 (Text-fig. 34) than it is in R192, R5829 and R5830 (Text-fig. 36). The coracoid groove is deeper in R196 (Text-fig. 35B) than it is in R5829

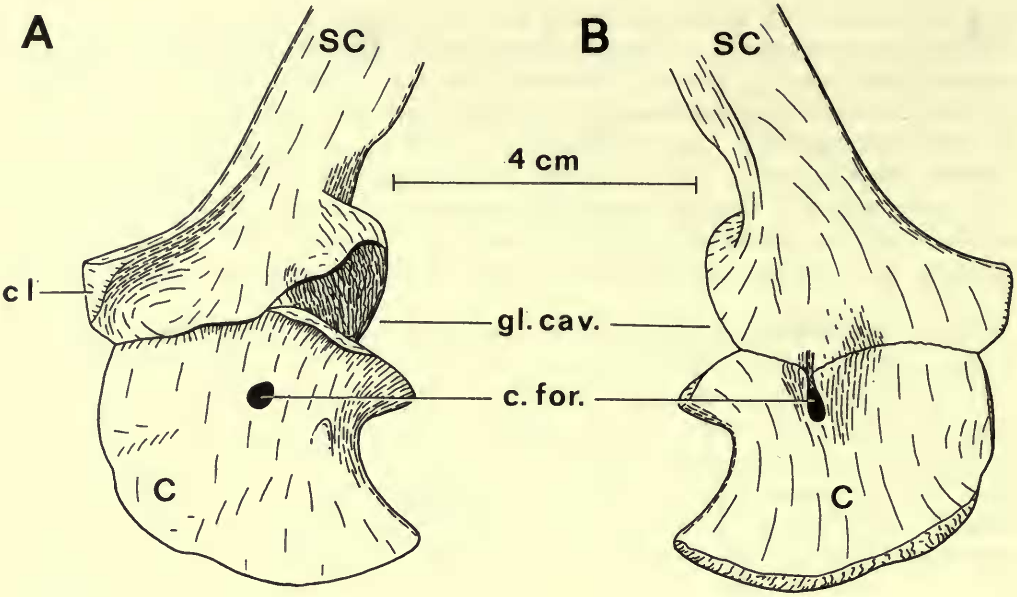


FIG. 35. *Hypsilophodon foxii.* Scapula and coracoid R196, × 1. A, ventro-lateral view; B, dorso-medial view. For abbreviations see Text-fig. 34.

or R5830. All these are random variations independent of size. The lateral edge running from the facet for the clavicle is strongly developed in R192, R196 (Text-fig. 34A) and R5829 but weakly so in R5830 (Text-fig. 36A). The sutural surface with the coracoid has well-developed ridges in R196 which are absent in R5830. The general curves of the scapula (and coracoid) of R196 (Text-figs. 34, 35) and R5829 are more strongly developed than in R5830 (Text-fig. 36); all these differences are probably due to the smaller size of R5830.

Coracoid. The coracoid is thin except for the dorsal part. The inner surface (Text-figs. 34B, 35B) is concave dorso-ventrally and convex antero-posteriorly, with a strongly developed depression on the antero-ventral part where the edge is very thin (Text-fig. 35B). Dorsally, the inner surface has a large raised area in the middle. The coracoid foramen (Text-fig. 35B), which extends diagonally forwards and downwards through the bone (visible in R5830), is located in the posterior part of this area. A well-marked groove (Text-fig. 35B) extends dorsally from the coracoid foramen and continues on to the scapula.

Sternum. The right sternal bone is longer than the left (Text-fig. 37), but this is presumably an individual variation. The antero-medial part is thick with an irregular sutural surface (Text-fig. 37D). Anteriorly the ventral and medial surfaces are covered with large bumps (Text-fig. 37B). The anterior edge is rounded medially but becomes sharp-crested laterally. The bone behind this edge is moderately thick

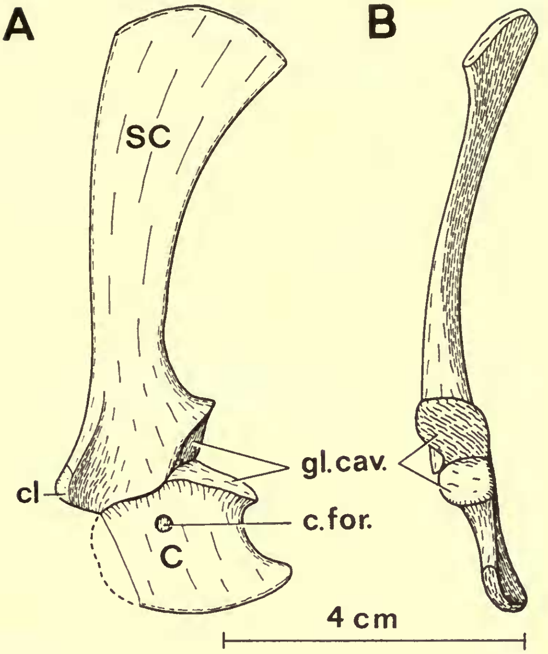


FIG. 36. *Hypsilophodon foxii.* Scapula and coracoid R5830, × 1. A, lateral view; B, posterior view. For abbreviations see Text-fig. 34.

as is the postero-lateral edge. The latter edge has an irregularly pitted surface that contacted the ends of the sternal sections of the first three dorsal ribs (Text-figs. 37B, E). The postero-medial part of the sternum is very thin.

ii) THE FORELIMB

Humerus. As a result of the twisting of the shaft (Text-fig. 38) the moderately expanded distal end of the humerus is set at an angle to the broader proximal end that carries the anteriorly directed delto-pectoral crest (Text-fig. 38E). This crest becomes progressively thicker distally towards the apex and the edge is rounded. In the region of the apex the crest has a flat surface, facing antero-laterally (Text-fig. 38D), which becomes rounded more distally to merge with the shaft. The broad proximal end with the delto-pectoral crest forms a longitudinally concave and transversely twisted anterior surface (Text-fig. 38C). Proximally the posterior edge is thin but it becomes thicker and rounded, forming a slight ridge where it meets the concave surface at the base of the delto-pectoral crest (Text-fig. 38C). This ridge continues on to the shaft, which is slightly oval in cross-section, and runs to the ventral ulnar condyle. The anterior intercondylar groove is wider, deeper and continues further along the shaft (Text-figs. 38D, F) than the posterior intercondylar groove (Text-figs. 38B, F).

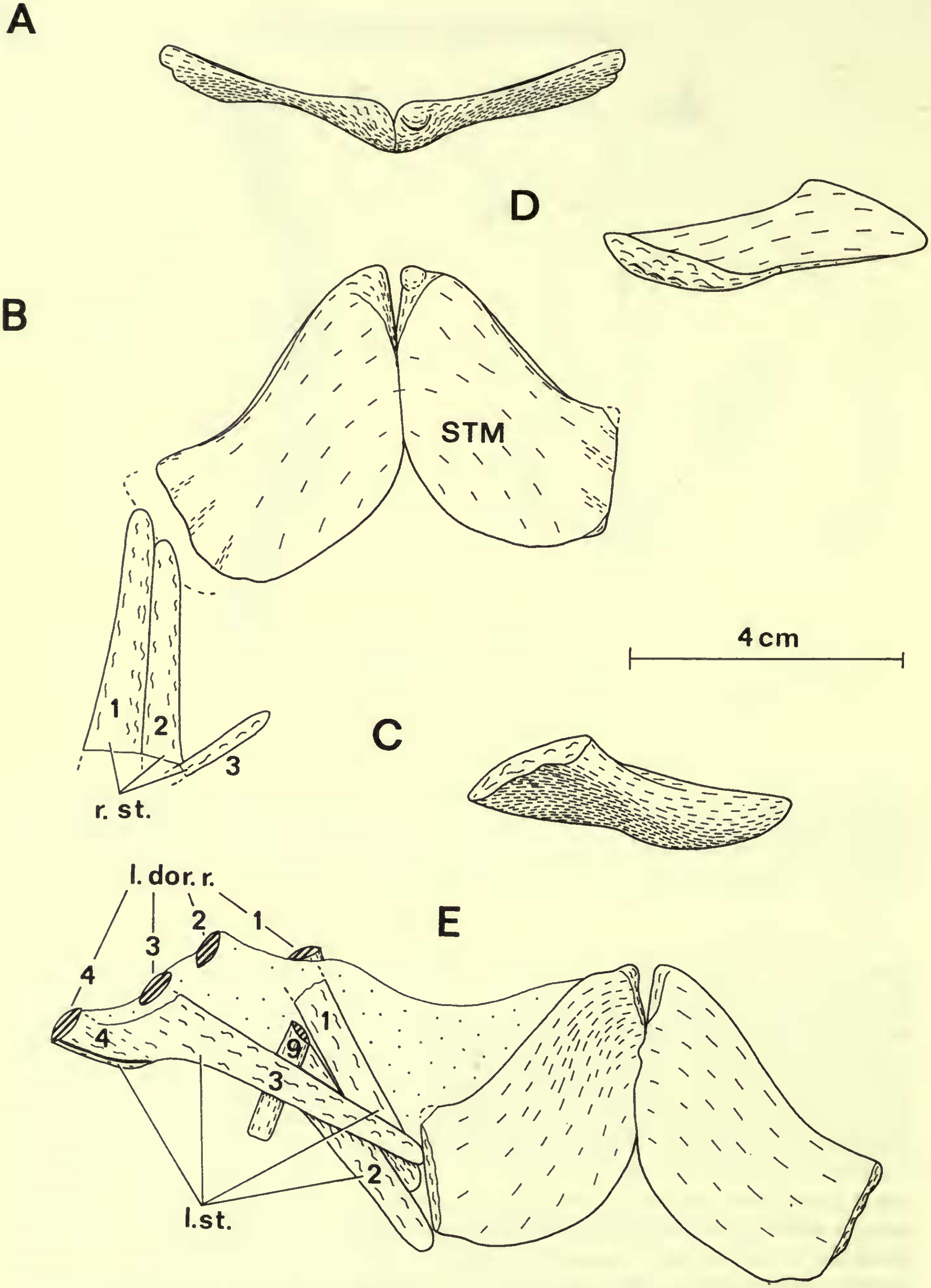


FIG. 37. *Hypsilophodon foxii*. Sternum R196, × 1. A, anterior view; B, ventral view with sternal section of dorsal ribs 1–3 displaced slightly; C, lateral view right sternal bone; D, medial view of right sternal bone; E, dorsal view with dorsal ribs 1–4. Abbreviations: STM, sternum; l dor r, dorsal ribs of left side; l st, sternal segments of left dorsal ribs; r st, sternal segments of right dorsal ribs.

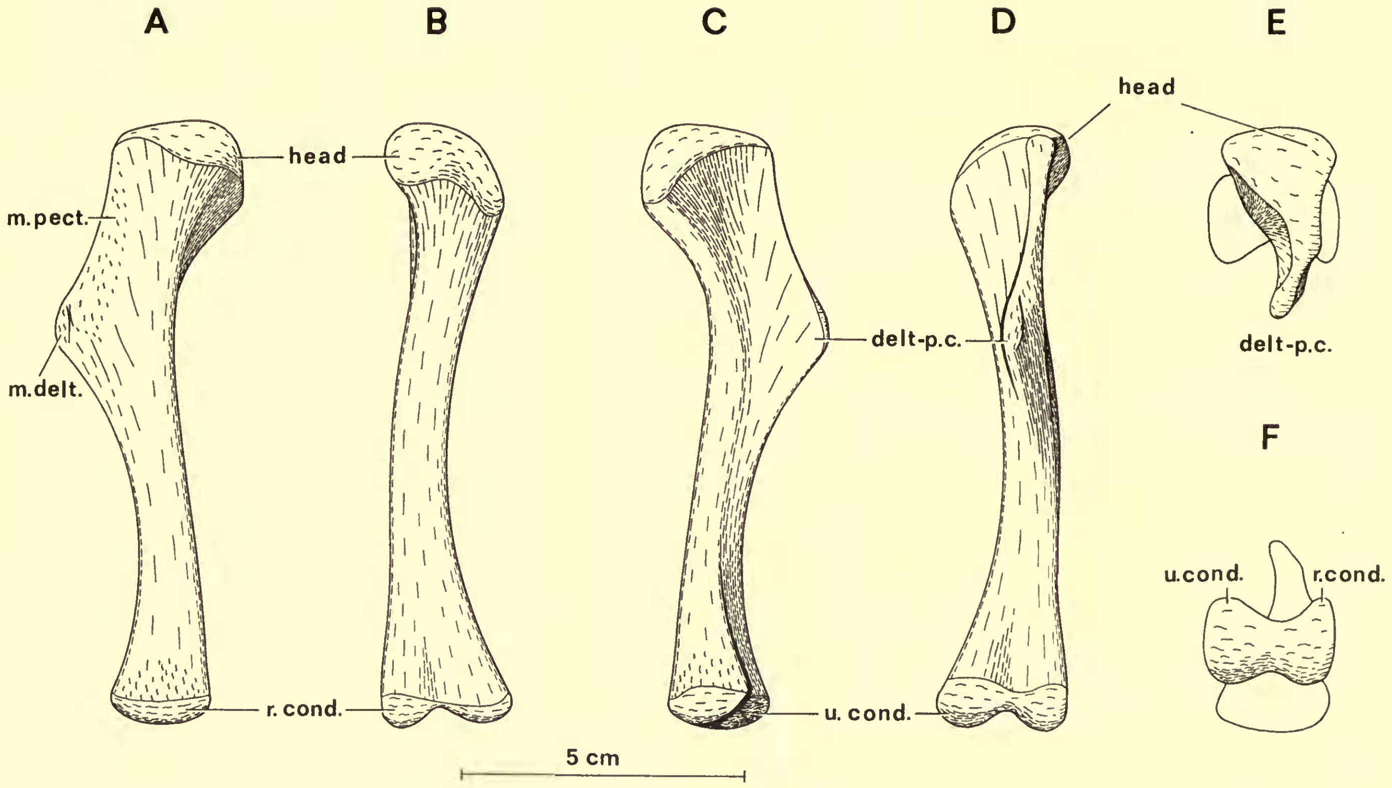


FIG. 38. *Hypsilophodon foxii.* Humerus R196, × ¾. A, lateral view ; B, posterior view ; C, medial view ; D, anterior view ; E, proximal view ; F, distal view. Abbreviations : delt-p.c, deltopectoral crest ; m delt., M. deltoideus ; m pect., M. pectoralis ; rc or r cond., radial condyle ; uc or u cond., ulnar condyle.

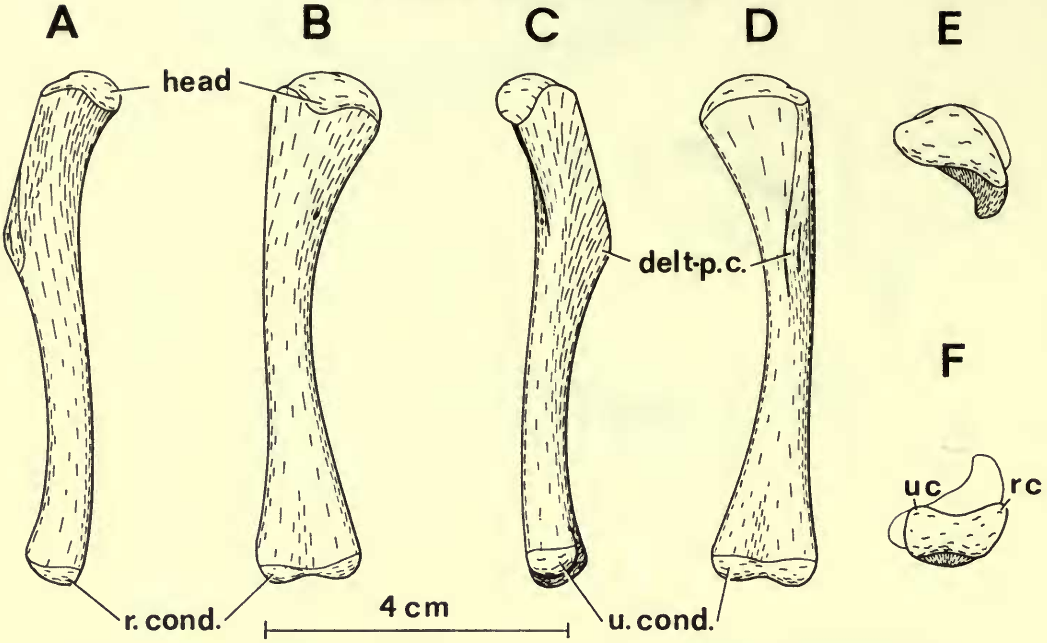


FIG. 39. *Hypsilophodon foxii.* Humerus R5830, × 1. Views and abbreviations as in Text-fig. 38.

The shaft is more twisted in R196 (Text-fig. 38) and R5829 than it is in the smaller R5830 (Text-fig. 39). A comparable difference occurs between small, medium-sized and larger humeri in *Protoceratops* (Brown & Schlaikjer 1940, fig. 27), so this is probably an age variation.

Ulna. The olecranon process is moderately well developed. The edges of the proximal end (Text-fig. 40E) continue along the tapering shaft to the slightly expanded and somewhat compressed distal end. The shaft is roughly triangular in cross-section with a slightly concave medial surface which becomes more strongly so distally (Text-figs. 40C, E). The dorsal ridge (Text-figs. 40D, E) continues to the thick and rounded antero-lateral (radial) edge of the distal end. The rounded medial edge (Text-figs 40C, E) continues to the sharp postero-medial edge of the distal end. The larger lateral edge continues as a well-defined edge on the outside of the shaft but merges with the convex lateral face of the distal end. The middle part of the shaft anterior to this ridge is slightly concave. Proximally there is a well-defined rugose bump (u, Text-fig. 40) while distally there are two rugose areas (v, w, Text-fig. 40).

Swinton (1936, fig. 6) figured the ulna and radius of R5830; he stated (: 564) that 'the right ulna . . . is preserved in perfect condition' and gave the length of the radius (: 566) and ulna (: 565). However, the forearm on both sides is represented only by proximal ends with that of the right radius mounted as a distal end. There are several odd distal ends in the Hooley Collection that have been referred to R5830, but none of these definitely fits on to the bones from the mounted skeleton.

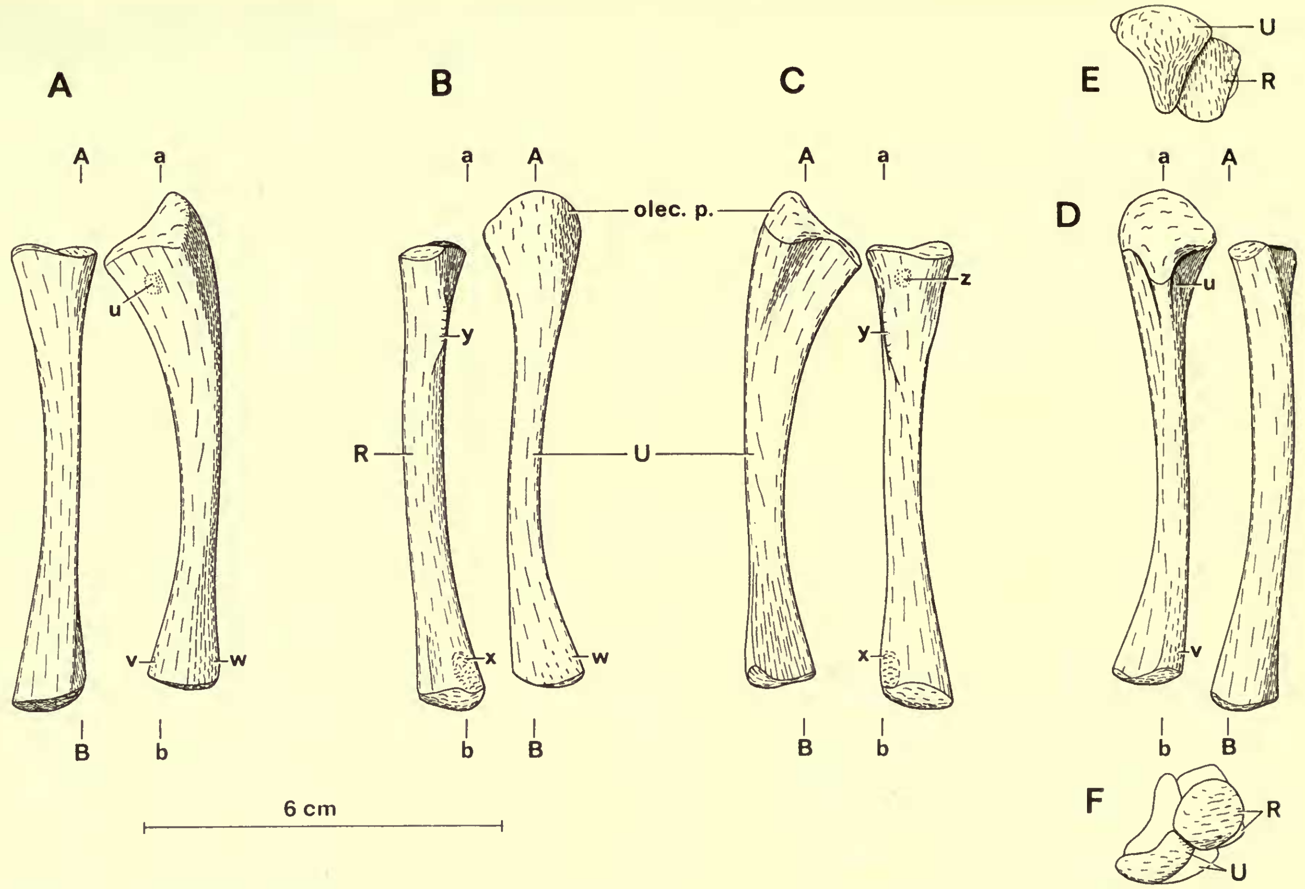


FIG. 40. *Hypsilophodon foxii.* Radius and ulna R196, × ¾. In views A–D the radius and ulna have been separated – for natural articulation superimpose line AB on ab in each case. A, lateral view; B, ventral or posterior view; C, medial view; D, dorsal or anterior view; E, proximal view; F, distal view. Abbreviations: olec. p., olecranon process; R, radios; U, ulna; u, v, w, x, y, z, areas with rugose surface markings.

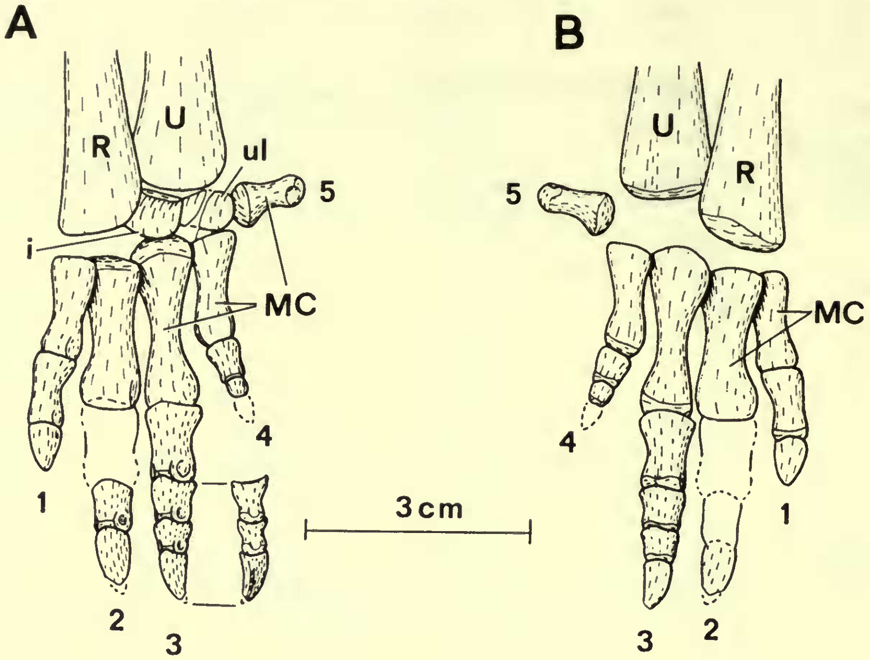


FIG. 41. *Hypsilophodon foxii.* Manus R196, ×1. A, dorsal view; B, ventral view. Abbreviations: MC, metacarpal; R, radius; U, ulna; 1–5, digits; i, intermedium; ul, ulnare.

Radius. The articular surface on the proximal end is concave along one diagonal and convex across the other (Text-fig. 40E). The shaft is subtriangular in section. The medial edge in the middle of the shaft is sharp but it is more rounded proximally and distally. The lateral edge is very slight and gently rounded distally. Proximally there is a well-defined ridge with insertion markings (y, Text-figs. 40B, C) while distally there is a rugose area (x, Text-figs. 40B, C).

Carpals. As noted by Hulke (1882), the wrist of the only complete manus (Text-fig. 41) is traversed by a seam of carbonaceous material that has obliterated the radiale and distal carpals and bisected the ulnare. The dorsal surfaces of the *ulnare* and of the adjacent *intermedium* of R196 are transversely concave (Text-fig. 41A). As preserved, it is impossible to determine the shape of the ulnare. The distal surface of the intermedium is rounded transversely and probably articulated against the distal carpals. The only trace of a *distal carpal* in R196 is a small corner which is wedged medially between the ulnare and metacarpal IV (Text-fig. 41A). The space between the radius and metacarpals I and II may indicate the outline of the *radiale*.

Three rather distorted carpal bones were obtained from the disarticulated partial manus of R2473 (Hulke 1873, pl. 18, fig. 3). These were matched with elements in the Hooley Collection that have now been referred to R5830. The *intermedium* corresponds closely with that of R196. The dorsal (Text-fig. 42a) and ventral

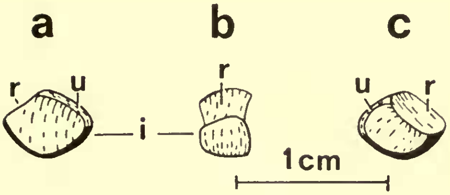


FIG. 42. *Hypsilophodon foxii.* Intermedium R5830, × 2. a, dorsal view; b, lateral view; c, ventral view. Abbreviations: i, intermedium; r, surface for radius; u, surface for ulna.

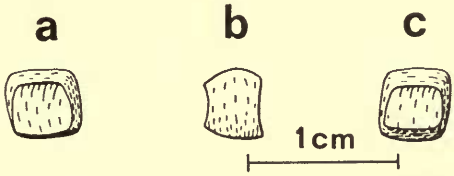


FIG. 43. *Hypsilophodon foxii.* Bone 1, R5830, × 2. Views as in Text-fig. 42.

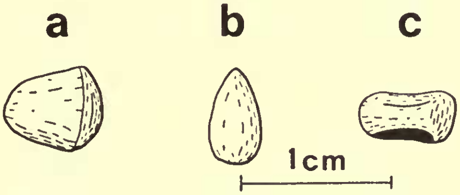


FIG. 44. *Hypsilophodon foxii.* Bone 2, R5830, × 2. Views as in Text-fig. 42.

(Text-fig. 42c) surfaces are transversely concave with a polished surface. The surface for the radius (r, Text-fig. 42) is concave but the remaining surfaces are convex laterally and transversely. These slope slightly inwards as the ventral surface is slightly smaller than the dorsal. The other two bones have been tentatively orientated as shown in Text-figs. 43 and 44. The second bone is a cube with a transversely concave dorsal surface and a similar but slightly smaller ventral surface (Text-figs. 43a, c). The four articular sides are gently convex laterally and transversely. This bone is either the radiale or the ulnare. The third bone has an irregular shape (Text-fig. 44) without the polished surfaces of the intermedium and the second bone; in this it resembles the distal tarsals.

Hulke (1882, pl. 79) showed the space in the wrist of R196 bounded proximally by the radius, intermedium and ulnare and distally by metacarpals I, II and III. Abel (1911, fig. 12) in his reconstruction closed this space so that there is practically no room for the radiale and none for any distal carpals. In contrast Steiner (1922, fig. 17) put the radiale and two distal carpals in this space, with a small first distal carpal and a second which is larger than the ulnare. Though Steiner's figure is

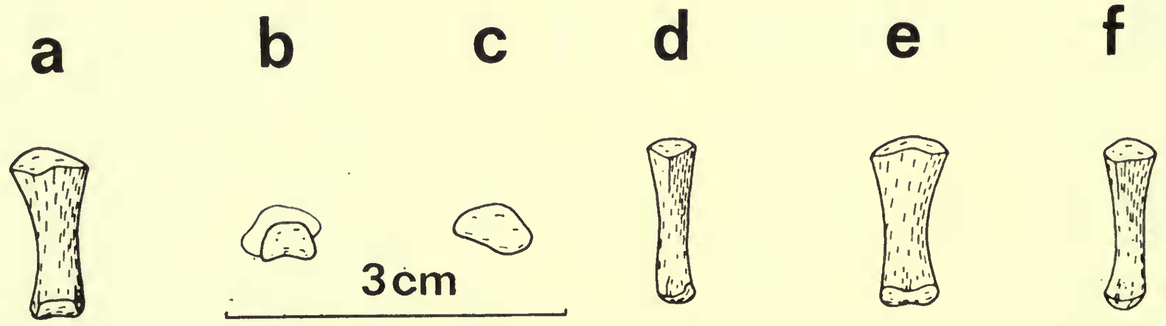


FIG. 45. *Hypsilophodon foxii.* Third metacarpal R5830, × 1·5. a, dorsal view; b, distal view; c, proximal view; d, lateral view; e, ventral view; f, medial view.

'after Hulke', Hulke did not in fact indicate these details. Heilmann (1926, fig. 116) showed a radiale and the dotted outline of four distal carpals. In *Thescelosaurus*, the two distal carpals are equal in size and much smaller than the ulnare (Gilmore 1915, fig. 11). However, if the second bone (Text-fig. 44) is a distal carpal then Steiner's reconstruction (1922) may be correct.

Metacarpals. The third metacarpal (Text-fig. 45) has a well-rounded proximal end with well-defined lateral and medial edges. The shaft in cross-section is a circle slightly flattened dorso-ventrally. The muscle grooves on the distal condyles are not strongly developed. There is no dorsal intercondylar groove and the ventral one is shallow. The size and shape of the metacarpals are shown in Text-fig. 41. As preserved the distal ends of metacarpals I, II, and III are inclined at an angle of about 45 degrees to a line through the carpus. The proximal ends are inclined at a slightly steeper angle and, though the area of contact is small, they are packed together. The proximal end surface of metacarpals II and III are rounded and slope. Metacarpal III is more slender and longer than metacarpal II. The proximal end of metacarpal IV is triangular and the condylar region is in the same plane as the carpus. Metacarpal V as preserved is set at quite an obtuse angle to the others but in life this was probably less marked.

Phalanges. The phalangeal counts of the first three digits are definitely 2, 3 and 4 respectively. The fourth metacarpal bears two phalanges and Hulke (1882) noted that the distal half of the second of these was missing, as was the continuation of the digit. Further development has exposed the ventral surface and the distal articular surface is practically complete so that only a small part of this phalanx is missing. Metacarpal V has a distal condyle but there is no evidence concerning the number of phalanges. Gilmore (1915 : 600) tabulated the phalangeal formula of *Hypsilophodon* as 2, 3, 4, 3, 2. This may be correct but the evidence from specimen R196 suggests the formula 2, 3, 4, 3 (? +), 1 (? +).

iii) THE PELVIC GIRDLE

Ilium. In external view (Text-figs. 46A, 48, 49) the dorsal part of the ilium of *Hypsilophodon* forms a thin and almost flat sheet of bone ; ventrally the bone is much thicker and the surface curves outwards to the acetabulum. The dorsal edge is sharp with a bevel running along most of its length. The posterior edge is rather square in section with a rugose surface while the postero-ventral edge is sharp. The anterior process of the ilium curves outwards with the lateral surface facing slightly dorsally (Text-figs. 50A, 51A). This curvature enabled the process to clear the adjacent ribs, provided a larger insertion area for part of the M. dorsalis trunci and permitted a more fore-and-aft action of the M. ilio-tibialis 1 (Text-fig. 49, see Galton 1969). In addition the amount of antero-ventral curvature varies a great deal between individuals ; the ilia can be arranged in a series that shows a progressive increase in the degree of curvature (Text-figs. 49A, 46A, 48A and 48B). This variation is independent of the sacral type because only R196 has a pentapleural sacrum. The outer edge of the ventral margin of the anterior process is rounded in all specimens, but the inner edge is more variable. In R196 (Text-figs. 51B, C) it is rounded

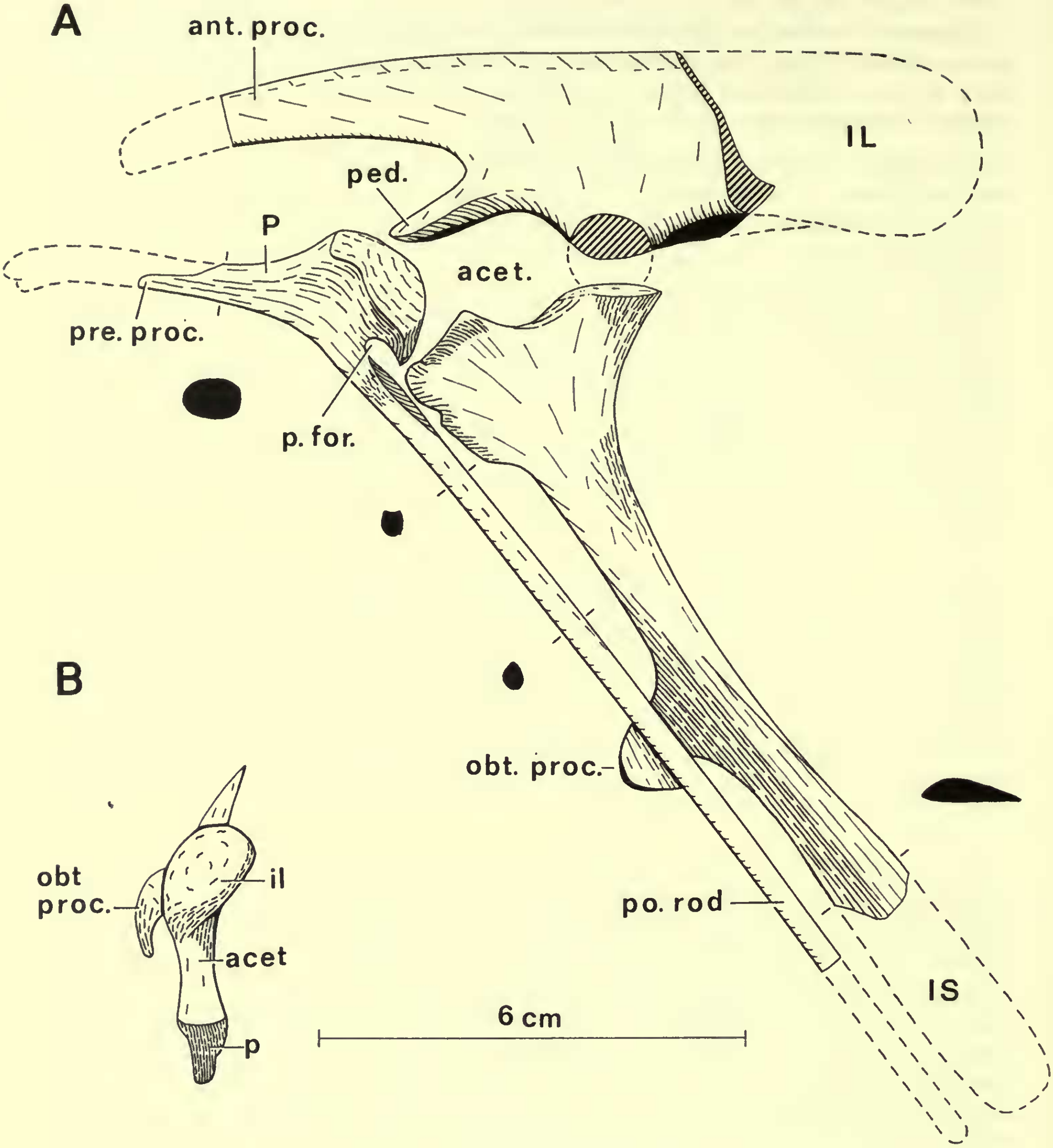


FIG. 46. *Hypsilophodon foxii*. Pelvic girdle R195, × 1. A, lateral view ; B, acetabular view of ischium. Abbreviations for Text-figs. 46–53. IL, ilium ; IS, ischium ; P, pubis ; acet., acetabulum ; ant. proc. or a. p., anterior process ; brev. sh., brevis shelf ; il., surface for ilium ; is., surface for ischium ; obt. p., obturator process ; p., surface for pubis ; ped., peduncle ; p. for., pubic foramen ; po. rod., post-pubic rod ; pre. proc., prepubic process.

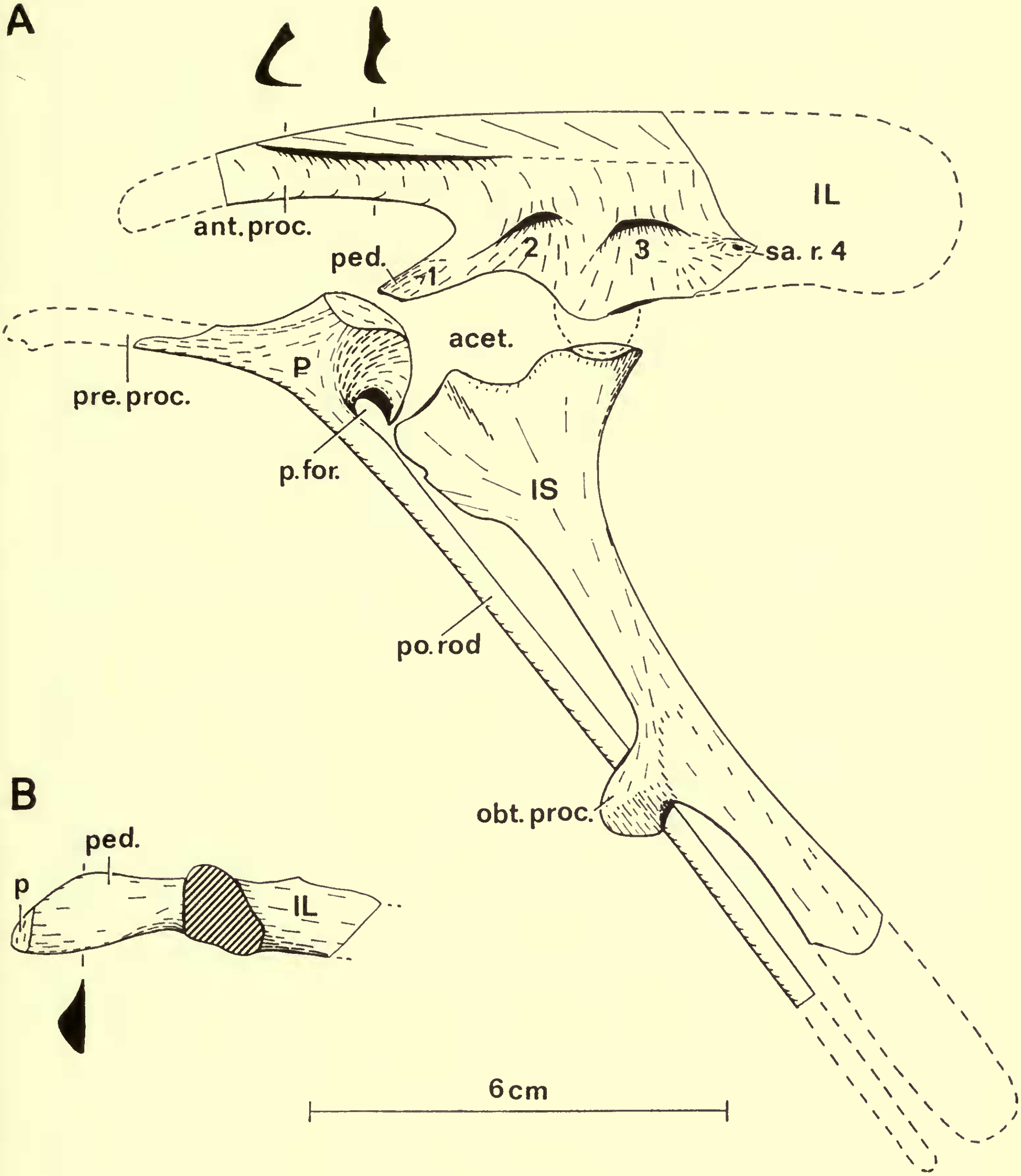


FIG. 47. *Hypsilophodon foxii.* Pelvic girdle R195, × 1. A, medial view ; B, acetabular part of the ilium. For abbreviations see page 84.

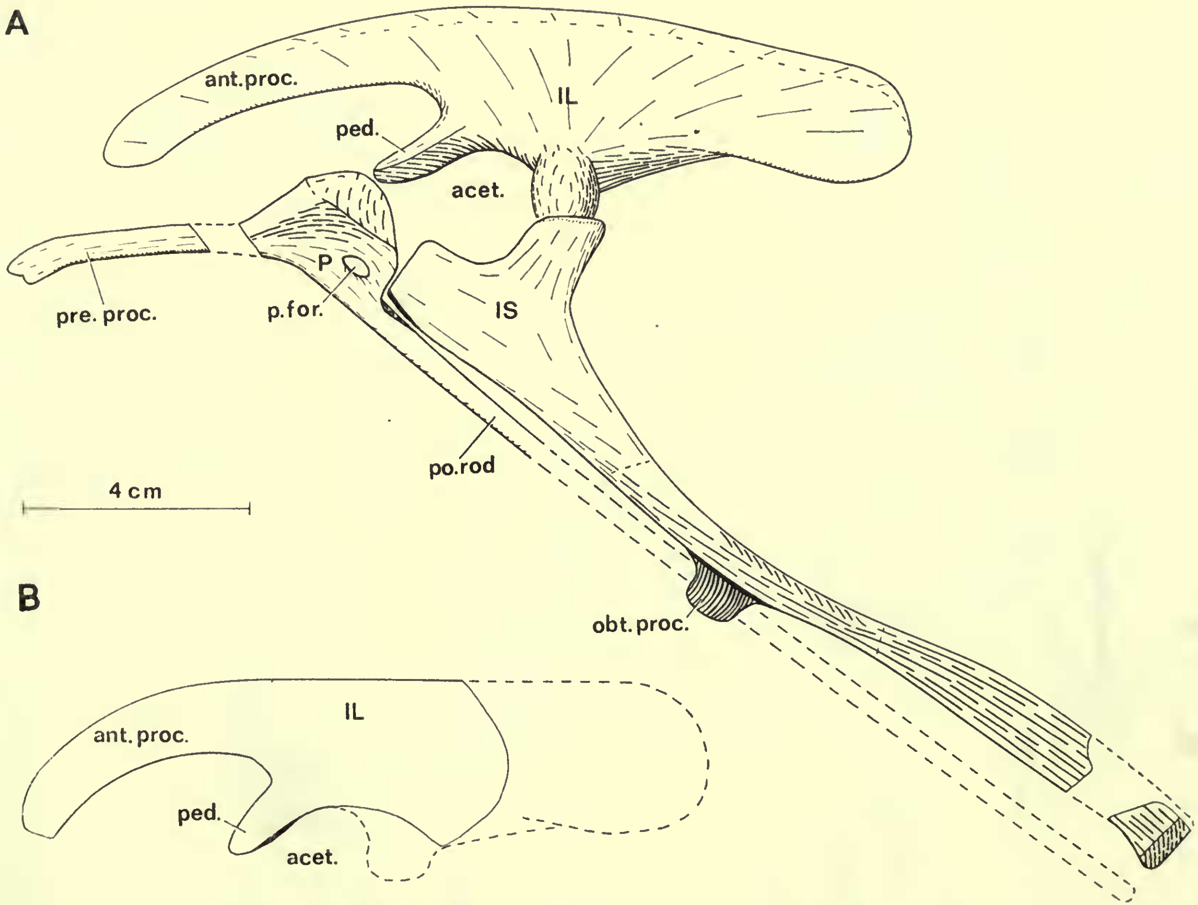


FIG. 48. *Hypsilophodon foxii*. A, pelvic girdle R196, $\times \frac{3}{4}$, lateral view ; B, ilium R2477a, $\times \frac{3}{4}$, lateral view. For abbreviations see page 84.

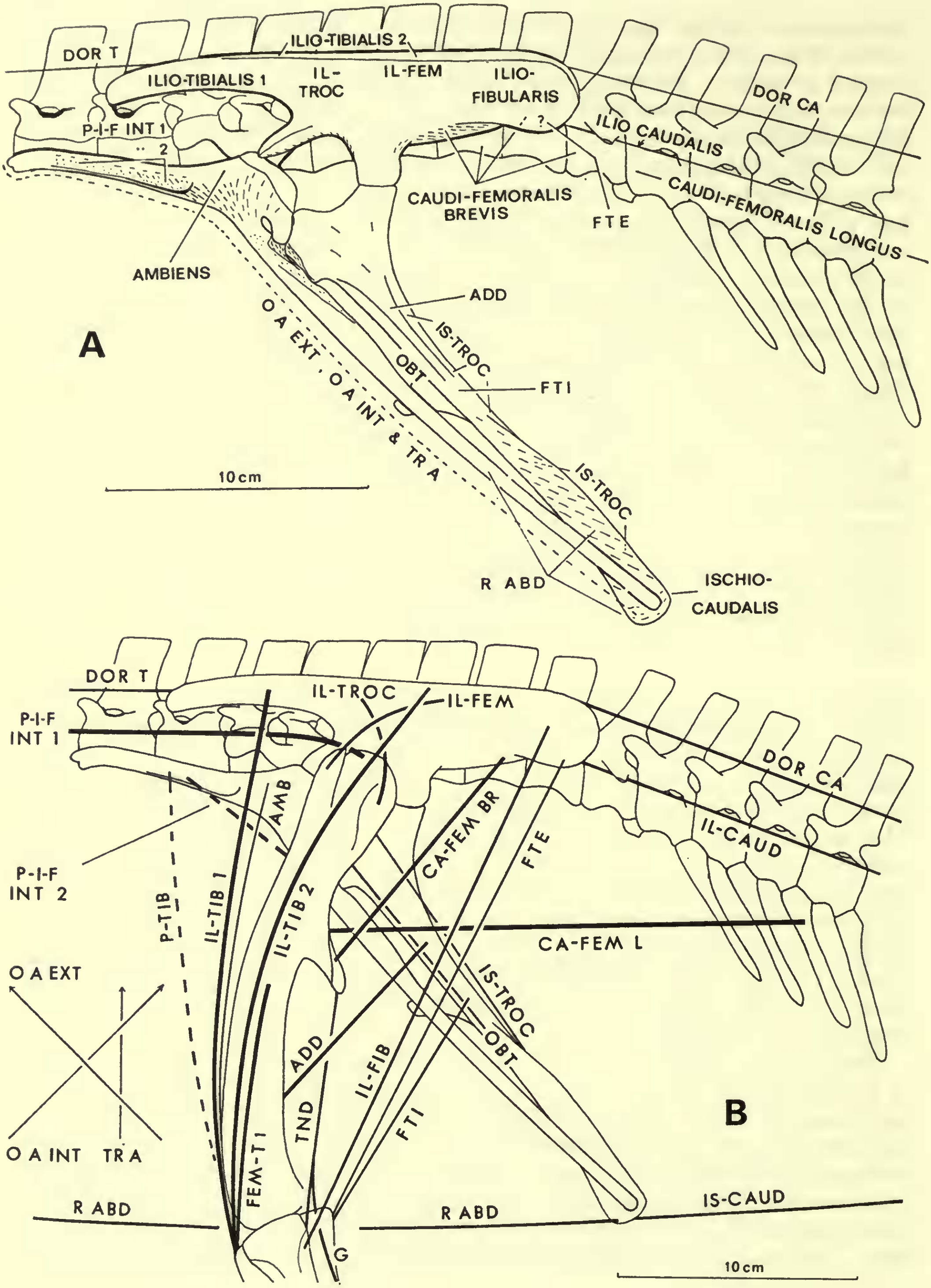
and somewhat thicker than the rest of the process. In R2477a the inner part forms a small ledge, which in R193 (Text-figs. 50B, C), R2477b and R195 (Text-fig. 47A) shows a progressive increase in size. This ledge is mainly sharp-edged, though it becomes reduced and rounded both anteriorly and posteriorly. This variation too is independent of the sacral type. The slender anterior peduncle is triangular in section with a sharp outer edge (Text-fig. 47B) which disappears posteriorly. Its ventral surface is broad and flat. It is broader in forms with the hexapleural sacrum (Text-figs. 47B, 50C) than in those with the pentapleural type (Text-figs. 51C, R2477b).

A prominent ridge runs along the medial surface (Text-figs. 47A, 50B, 51B) of the anterior process. Ventral to this there is a longitudinal depression which is bordered by the internal ledge mentioned above. Anteriorly another, much smaller, ridge runs diagonally across the process. The thicker ventral region of the ilium bears the rugose facets for the sacral ribs. The ledge below these sacral facets is sharp-edged except for the section that lies internal to the ischiadic head of the ilium.

In all the ilia the first sacral rib fits on to the dorso-medially facing inner surface of the peduncle. The facets for the remaining sacral ribs are more anteriorly placed in R196 (Text-fig. 51B) than they are in R193 (Text-fig. 50B) and R195 (Text-fig. 47A), both of which have a hexapleural sacrum. In both types there is a projecting edge above facets 2 and 3. There is a similar edge above facet 4 in R196 but this facet is only partly on the brevis shelf (Text-fig. 51). In R195 the whole facet is on the brevis shelf and, anteriorly at least, there is a dorsal edge (Text-fig. 47A). In R193 there is no dorsal edge and the facet is obliquely inclined (Text-fig. 50), in contrast to its much more vertical position in the others.

Pubis. The anterior end of the pubis is slightly flattened (Text-fig. 48A). The outer surface of the prepubic process is flat with well-developed striations (Text-fig. 49) and the ventral edge is grooved. The function of the prepubic process has been discussed elsewhere (Galton 1969, 1970a) and it was suggested that the striations were for a limb muscle (M. ilio-femoralis internus, M. pubo-tibialis or M. ambiens). The ventral part of the stout acetabular region is laterally constricted and has a rounded ventral edge (Text-fig. 52B). The outer surface (Text-figs. 46A, 48A, 49A) is hollowed anteriorly into a shallow and approximately circular depression, but above the obturator foramen this surface is convex. The inner surface (Text-fig. 47A) is slightly concave anteriorly, but it is convex at the root of the post-pubic rod. Posteriorly the inner surface is strongly concave and funnels into the obturator foramen (Text-fig. 47A). The postero-dorsal articular region is rough-textured and, except anteriorly, is sharp-edged.

The obturator region is variable. Among the smaller individuals there is a notch in R195 (Text-fig. 47A) but a foramen in R196 (Text-fig. 48A) ; among the larger individuals there is a notch in R5829 but a foramen in R193 (Text-fig. 49A). It is apparent that this is an individual variation. In those specimens where closure of the notch has occurred, R196 shows no trace of a suture, while in R193 a suture is visible on the lateral surface only ; in the latter specimen there is no evidence as to when closure occurred (growth stages of the same individual would be needed for this). Anteriorly the post-pubic rod has a dorsal sheet which may be variously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developed. In R196 it is absent (Text-fig. 48A) ; in R195 it is small and faces dorso-medially (Text-figs. 47A, 48A) ; in R5829 it is larger ; and in R193 it is very well developed (Text-fig. 49A). The edge is thickened in R193, forming with the most anterior part a triangular area with an irregular surface.

Ischium. The ischium consists of a proximal head-region which is separated from the large flat blade region by a constricted shaft (Text-figs. 46A, 48A, 49A, 53). Ventrally the head and shaft merge in R196 (Text-fig. 48A) and R5830 (Text-fig. 53E) but this junction becomes progressively more marked in the series R5829, R195 (Text-fig. 46A) and R193 (Text-fig. 49A). This is probably an individual variation. The shaft is twisted so that the blade is at an angle of about 45 degrees to the head. The inner surface of the blade therefore faces dorso-medially. This surface and the internal surface of the head meet along a diagonal line which continues distally on to the base of the obturator process (Text-fig. 47A). In relation to the rest of the ischium the acetabular region is longer in R196 (Text-fig. 48A) than it is in R193 (Text-fig. 49A) or R195 (Text-fig. 46A) and the ventral part is lengthened to a corresponding degree. At the anterior end of the acetabular region there is an internal expansion which is more strongly developed in R196 (Text-fig. 53D) than in R195 (Text-fig. 46B). The internal surface below this process forms a shallow depression.

The dorsal edge of the shaft is rounded. Ventrally, the shaft is sharp-edged and distally this edge curves abruptly downwards and inwards to form the obturator process (Text-fig. 47A). Posteriorly, the shaft gradually thins out as it merges into the blade region. This continuation of the shaft tends to cross from the outer to the inner edge because of the outward curve of the blade relative to the shaft. The distal part of the ischium is straight, flat and blade-like. Anteriorly, on the dorsal

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FIG. 49. *Hypsilophodon foxii.* A, pelvic girdle R193 in lateral view to show areas of attachment of the individual muscles. Data also from R196 and 28707. Figure from Galton (1969, fig. 6 ; see fig. 7 for stereo-photograph of pubis and ischium R193) in which the areas are described. B, reconstruction of the pelvic region showing the lines of action of the individual muscles. Data from R193, R196, R5830 and 28707. Figure from Galton (1969, fig. 4). Compare with Text-fig. 55.

The muscles have been abbreviated as follows :

ADD	M. adductor femoralis	IS-CAUD	M. ischio-caudalis
AMB	M. ambiens	IS-TROC	M. ischio-trochantericus
CA-FEM BR	M. caudi-femoralis brevis	LIG	ligaments for holding head in acetabulum
CA-FEM L	M. caudi-femoralis longus		
DOR CA	M. dorsalis caudae	O A EXT	M. obliquus abdominis externus
DOR T	M. dorsalis trunci	O A INT	M. obliquus abdominis internus
FEM-T 1, 2 & 3	M. femoro-tibialis 1, 2 and 3	OBT	M. obturator internus
F T E	M. flexor tibialis externus	P-I-F INT 1	dorsal part of M. pubo-ischio-femoralis internus
F T I	M. flexor tibialis internus		
G	M. gastrocnemius	P-I-F INT 2	ventral part of M. pubo-ischio-femoralis internus
IL-CAUD	M. ilio-caudalis		
IL-FEM	M. ilio-femoralis	P-TIB	M. pubo-tibialis
IL-FIB	M. ilio-fibularis	R ABD	M. rectus abdominis
IL-TIB 1 & 2	M. ilio-tibialis 1 (sartorius) and 2	TND	tendon inserting on fibula
IL-TROC	M. ilio-trochantericus	TR A	M. transversus abdominis

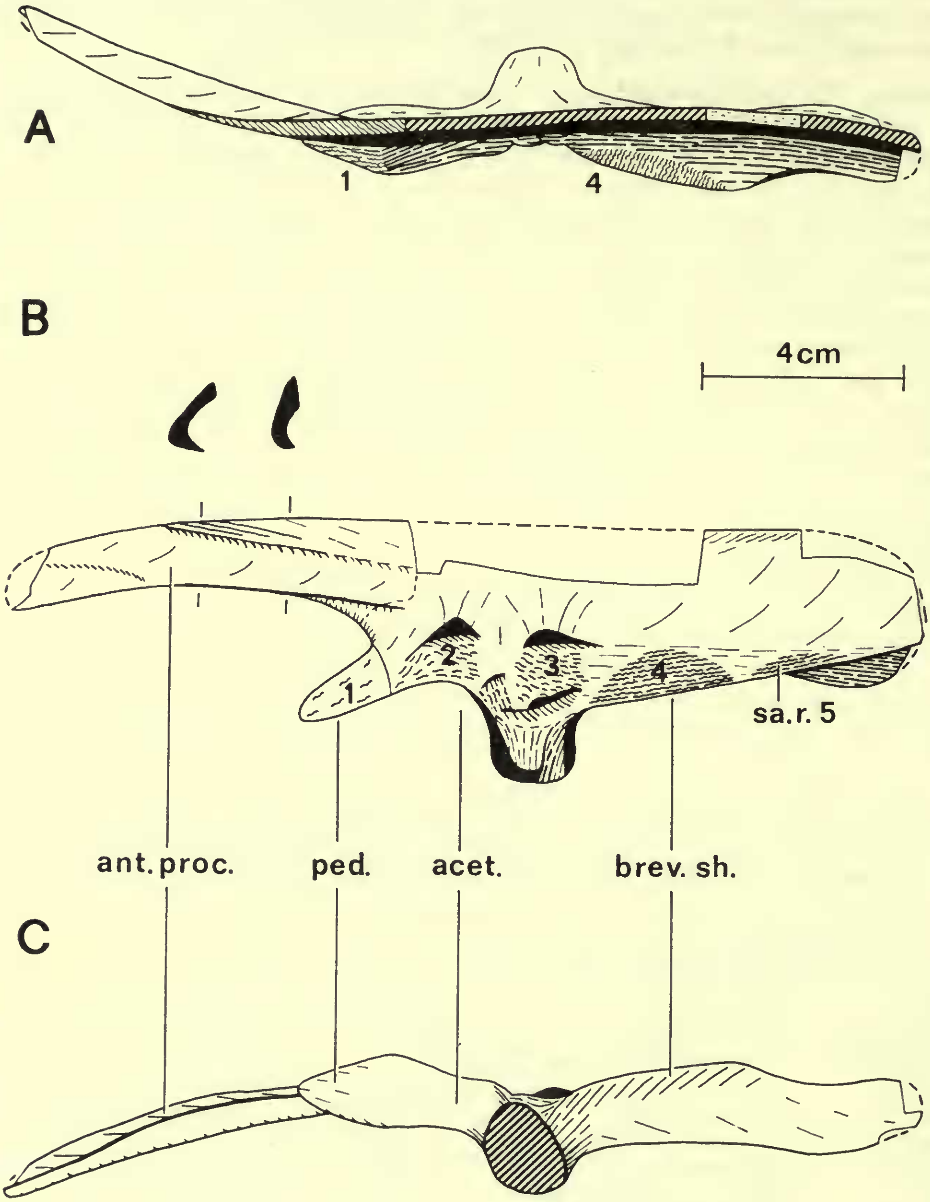

FIG. 50. *Hypsilophodon foxii*. Ilium R193, × ⅔. A, dorsal view; B, medial view; C, ventral view. For abbreviations see page 84.

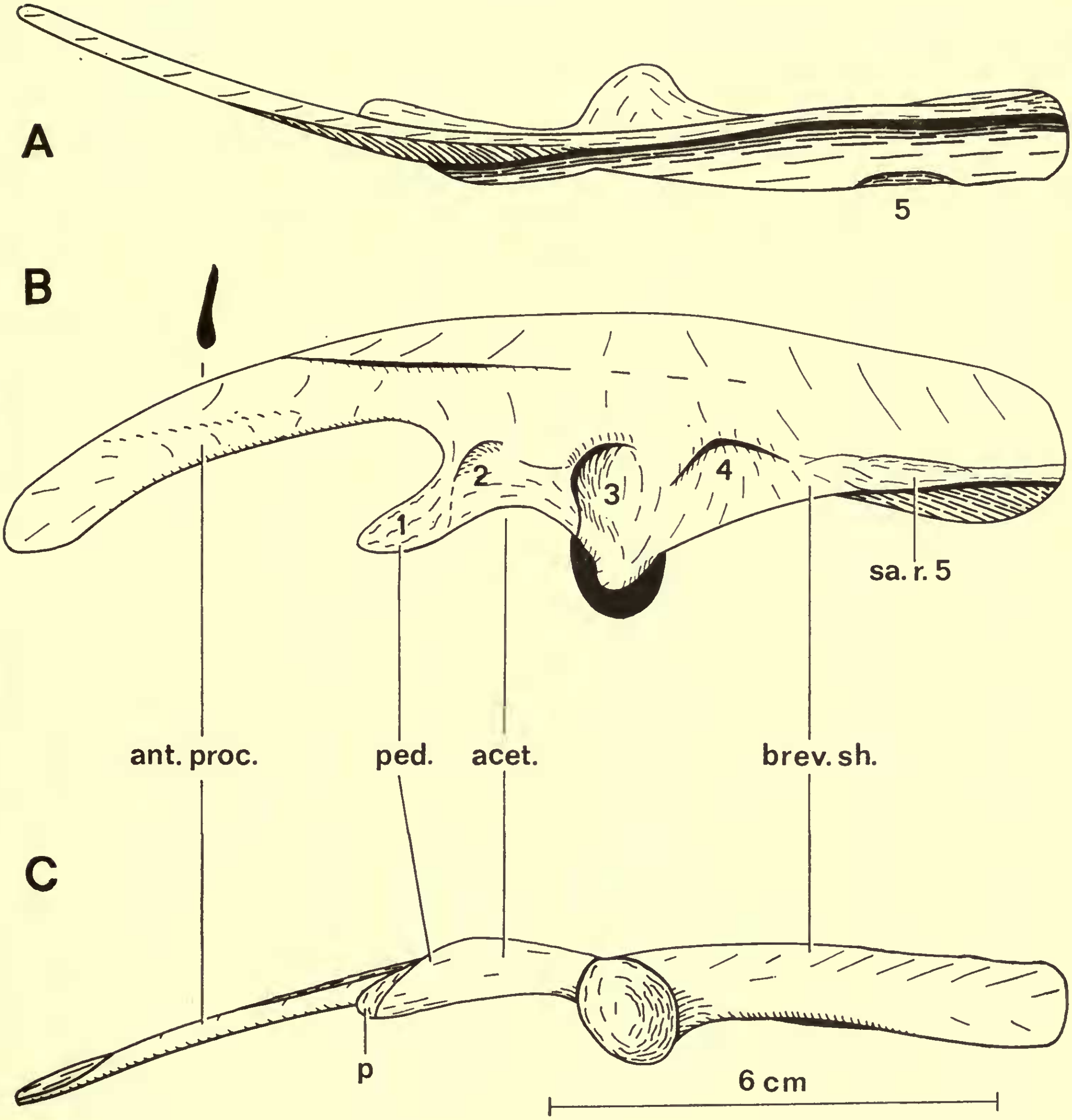

Fig. 51. *Hypsilophodon foxii.* Ilium R196, × 1. A, dorsal view; B, medial view; C, ventral view. For abbreviations see page 84.

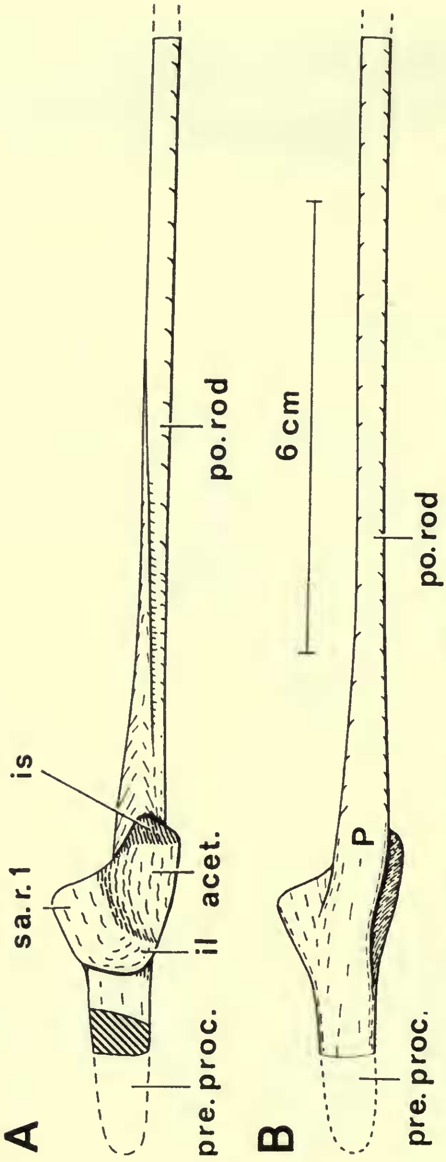

FIG. 52. *Hypsilophodon foxii*. Pubis R195, × 1. A, dorsal view; B, ventral view. For abbreviations see page 84.

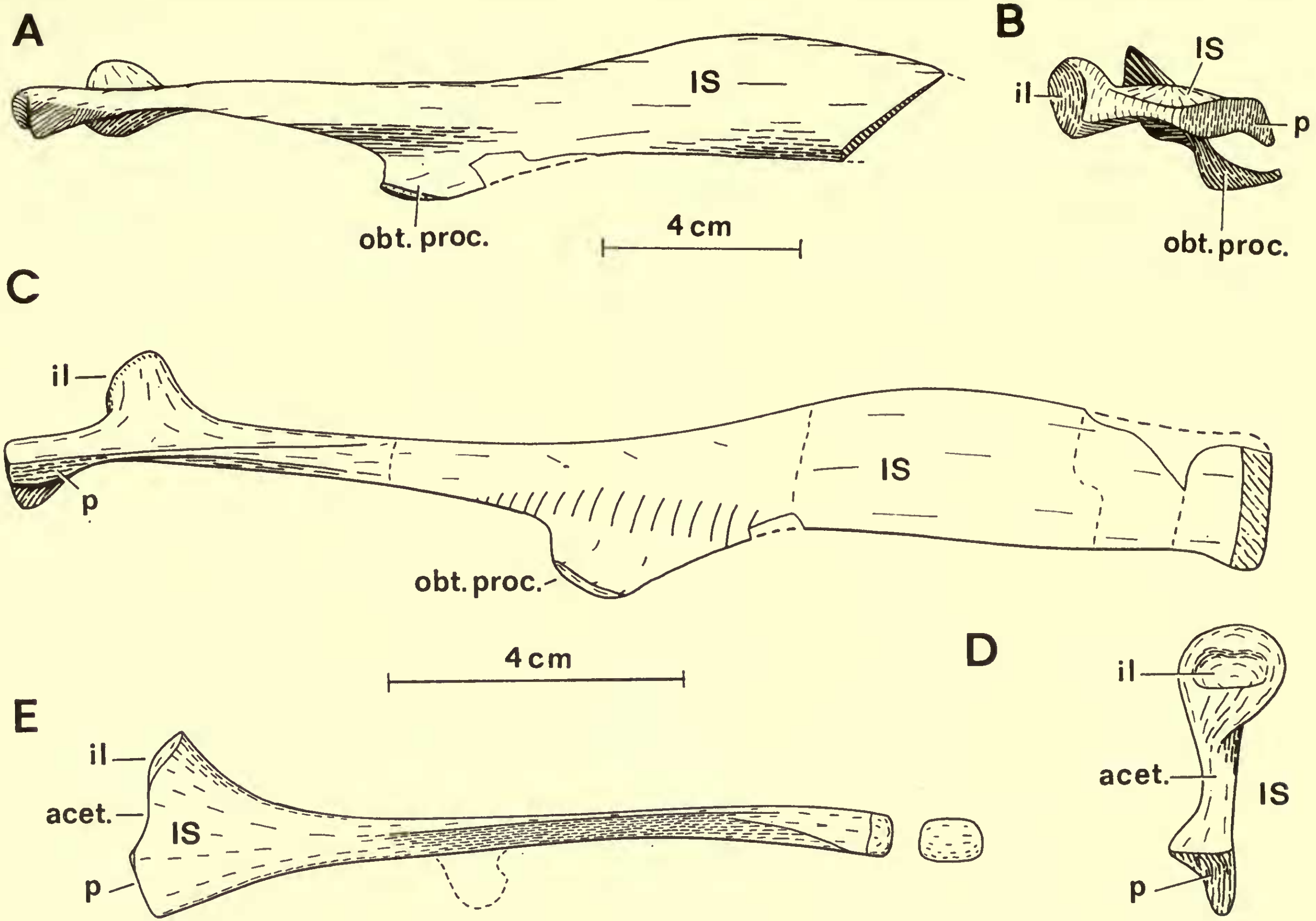

FIG. 53. *Hypsilophodon foxii.* Ischium R193, $\times \frac{2}{3}$. A, ventral view; B, proximal view. Ischium R196, × 1. C, ventral view; D, proximal view. Ischium R5830, × 1. E, lateral view. For abbreviations see page 84.

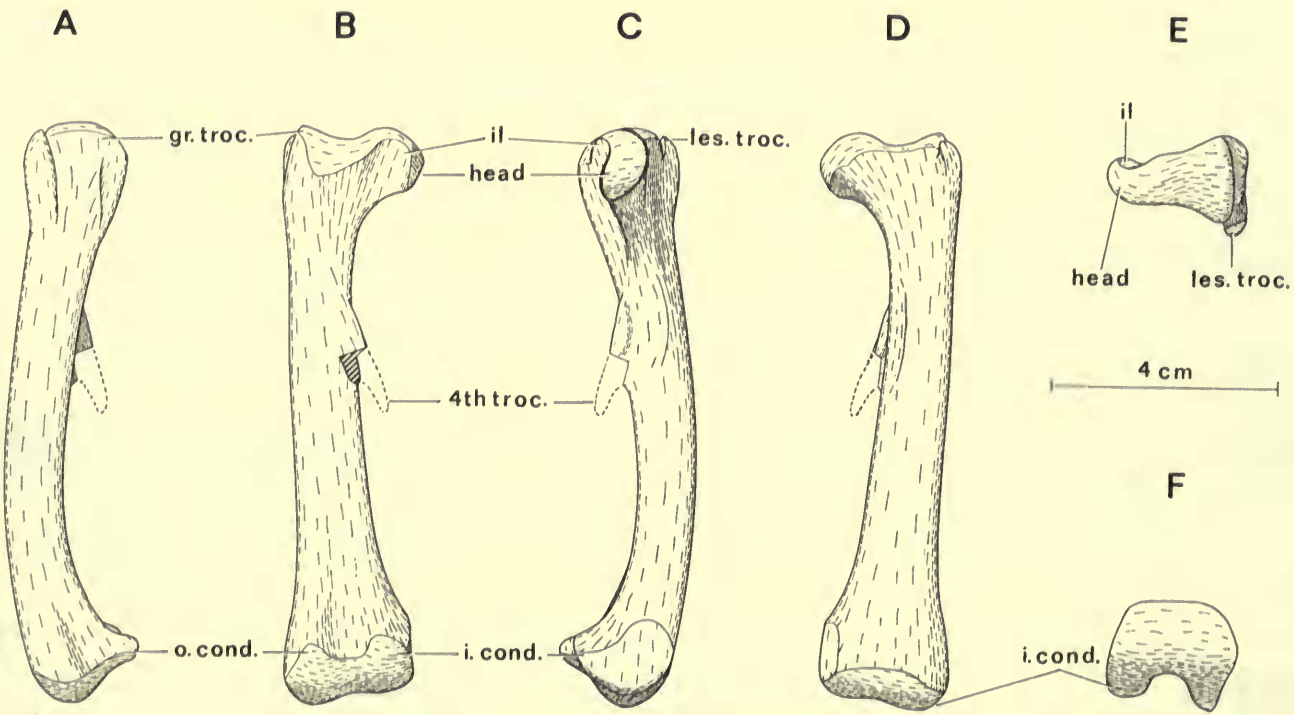

FIG. 54. *Hypsilophodon foxii.* Femur R5830, × ¾. A, lateral view; B, posterior view; C, medial view; D, anterior view; E, proximal view; F. distal view. Abbreviations: gr. troc., greater trochanter; i. cond., inner condyle; il., depression for ischiadic head of ilium; les troc, lesser trochanter; o. cond, outer condyle; 4th troc, fourth trochanter.

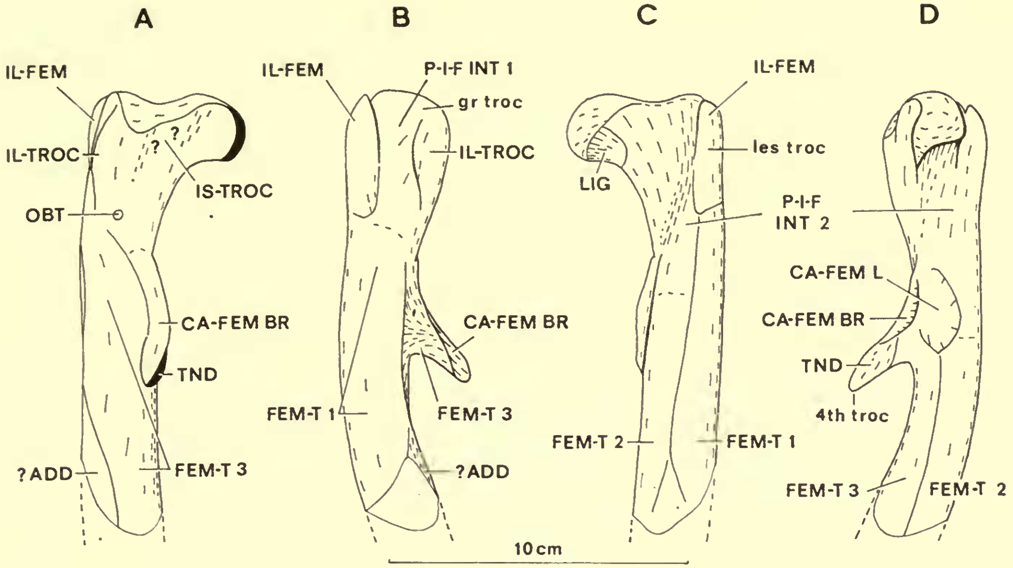

FIG. 55. *Hypsilophodon foxii*. Femur showing the areas of attachment of the limb muscles, mainly R193 with data from R196 and R5830. From Galton (1969, fig. 10; see fig. 8 for stereo-photograph of femur of R193) in which the areas are described. A, posterior view; B, lateral view; C, anterior view; D, medial view. Abbreviations: gr. troc., greater trochanter; les. troc., lesser trochanter; 4th troc, fourth trochanter. For abbreviations of muscles see Text-fig. 49.

surface of the blade, there is a definite depression above the obturator process (Text-fig. 47A). In R196 alone, a groove is present along the upper region of the outer surface of the blade. The dorsal edge of the blade is sharp. Ventrally, it is also sharp-edged, but it thickens distally to form an almost square edge. The distal end of the blade is swollen, with a rugose surface (Text-fig. 53E).

iv) THE HINDLIMB

Femur. The shaft of the femur is twisted so that the outer surface at the proximal end becomes the anterior surface more distally (Text-fig. 54D). The lesser trochanter is somewhat triangular in section (Text-fig. 54E) and is separated from the greater trochanter by a short cleft (Text-fig. 54D). The lesser trochanter is set slightly away from the external surface of the greater trochanter but gradually merges with the shaft more distally (Text-fig. 54A). Proximally the outer surface of the greater trochanter is flat but near the posterior edge there is an 'S'-shaped ridge that separated the insertion area of the M. pubo-ischiofemoralis internus 1 from the more posterior M. ilio-trochantericus (Text-fig. 55B; see Galton, 1969 in which the areas of muscle attachment on the femur of R193 are discussed). Running diagonally across the posterior face of the head is a strongly concave depression (Text-figs. 54B, E) which is bounded internally by a stout ridge.

Behind the head the neck and shaft form an acute though rounded edge which is continuous with the sharper outer edge of the pendant fourth trochanter pointing posteriorly. The large fourth trochanter probably improved the leverage of the M. caudi-femoralis brevis (from brevis shelf of ilium; Text-fig. 49) during the first half of femoral protraction (see Galton 1969). The outer surface (Text-fig. 55A) of the fourth trochanter is gently concave, the curve continuing that of the adjacent shaft. In internal view (Text-fig. 54C) most of the shaft is convex, but at the base of the fourth trochanter there is a depression, quite deep (R193, Text-fig. 55D; R195, R2477b) or very shallow (R196, R5829, R5830, Text-fig. 54C), which probably served for the insertion of the caudi-femoralis longus muscle (Text-fig. 55D; see Galton 1969). The shaft is narrowest just above the fourth trochanter where its cross-section is roughly quadrilateral with rounded edges. Below this it is roughly circular with a slight antero-posterior flattening. The anterior face (Text-fig. 54D) forms a progressively flatter convex curve and there is practically no anterior intercondylar groove (Text-fig. 54F). Posteriorly the outer condyle is almost as large as the inner and the surface becomes concave towards the base of the condyles with a deep but quite wide intercondylar groove (Text-figs. 54B, F).

Tibia. The proximal end is only moderately expanded (Text-fig. 56E) with a flat and slightly inclined surface (Text-fig. 56B). The proximal condyles (Text-fig. 56B) are rounded and approximately equal in size and they shortly merge with the convex shaft. The outer condyle bears a much smaller condyle on its antero-lateral face (Text-fig. 56A) against which the fibula fitted. The cnemial crest of the tibia is small and forms a rounded edge (Text-fig. 56D) which is continued somewhat diagonally down the shaft, passing internally to merge with the base of the inner malleolus (Text-fig. 56D). The depression between the distal malleoli continues along about a quarter of the shaft (Text-fig. 56D). In anterior view (Text-fig. 56D) the medial part of the inner malleolus is convex while the lateral part below the intercondylar groove is transversely concave and more obliquely inclined. In posterior view (Text-fig. 56B) there is a distal sharp edge backing the malleoli. The surface above the outer malleolus is convex but that above the inner malleolus is concave.

The shaft of the tibia is basically triangular in section but the sharpness of the edges varies. In R196, R752 and R5830 (Text-fig. 56) these edges are rounded apart from that above the outer malleolus. In R199 (Hulke 1882, pls. 80 and 81) the edges are more marked and the edge above the outer malleolus is much sharper and forms a step. The edge visible in anterior view above the inner malleolus also varies. In R193, R199 and R5830 (Text-fig. 56D) it is smooth, forming a gentle and continuous curve on the shaft. In R196 and R5829 this edge, about a third up, is considerably enlarged and swollen, the area being covered with well-developed surface markings. All of these seem to be individual variations.

Fibula. Only in R5830 are both ends well preserved. Swinton (1936: 568) noted that the right fibula of this specimen was complete and figured it as such (Swinton 1936, fig. 7) but the middle two-thirds is restored in plaster. The proximal surface is transversely rounded and articulated during adduction with the groove on the outer condyle of the femur. The concave curve of the medial surface (Text-fig. 56E) continues on to the proximal third of the shaft but below this the shaft is oval in cross-section. In S.M. 4127 the upper half of the fibula is slightly curved, with a concave anterior outline, and it is set at a slight angle to the distal half. Distally the fibula is backed to a progressively greater extent by the outer malleolus of the tibia. This part of the fibular shaft in R193 is laterally expanded with a sharp inner edge ; the anterior surface is slightly concave longitudinally while the posterior surface against the tibia is flat. The outer edge is gently convex and this, together with the anterior surface, sweeps out to the distal head ; the latter is rounded in outline apart from the flat area against the tibia. The edges of the distal end are rounded but the end surface is flat and fitted against the calcaneum.

Astragalus. This consists of two sheets of bone, one capping the distal end of the tibia (Text-fig. 57E), the other an ascending process that wraps round part of the anterior surface of the tibia (Text-figs. 56D, G). The ascending process ends in a tooth-like structure set out in slight relief from the adjacent bone (Text-figs. 56D, 57A, B). Below this ' tooth ' the ascending process is very thick and continues posteriorly as a broad ridge across the concave proximal surface (Text-fig. 57A) while medial to this ridge there is a large depression. This proximal surface was closely applied to the distal end of the tibia (compare Text-figs. 57A, 56F). The astragalus thins posteriorly and ends in a sharp edge (not visible in Text-fig. 56B) closely applied to the adjacent surface of the tibia. Though there is a gap below the inner corner of the fibula in R5830 (Text-fig. 56D) this area in R196 is filled by bone that appears to belong to the astragalus. This is confirmed by the presence of a broken surface on the external proximal corner of the astragalus of R5830 (Text-fig. 57D). The shape of this part of the bone is indicated by the adjacent surfaces of the fibula and calcaneum.

Calcaneum. The outer surface (Text-fig. 56A) is gently concave and forms a definite edge, indented in several places (Text-fig. 56E), with the curved antero-distal surface for distal tarsal 1. The proximal surface against which the fibula fitted is concave (Text-fig. 57A), the depression continuing medially on to the inner surface (Text-fig. 57C). The posterior surface for the outer malleolus of the tibia is a large depression (o, Text-figs 57C, D) which forms a thin and sharp edge with the outer edge (Text-fig. 57D). This obliquely inclined depression forms sharp diagonal edges with the proximal (Text-fig. 57A) and distal (Text-fig. 57E) surfaces. The medial view (Text-. fig. 57C) shows five surfaces, three of which I have designated (f, d.2 and o). The surface (a) for the main part of the astragalus is flat and above this there is a concave surface (e) for the dorso-laterally directed process of the astragalus. A medially directed corner (see Text-fig. 57A) is formed by the contact edges of surfaces e, f and o. However, the antero-distal part of the depression (e) is also continuous with those surfaces for the fibula (f) and tibia (o).

Distal tarsal 1. This is an irregularly flattened plate of bone with rounded edges which are indented in several places. Most of the proximal surface (Text-fig. 57F) with which the astragalus articulated is slightly convex, apart from a central concave

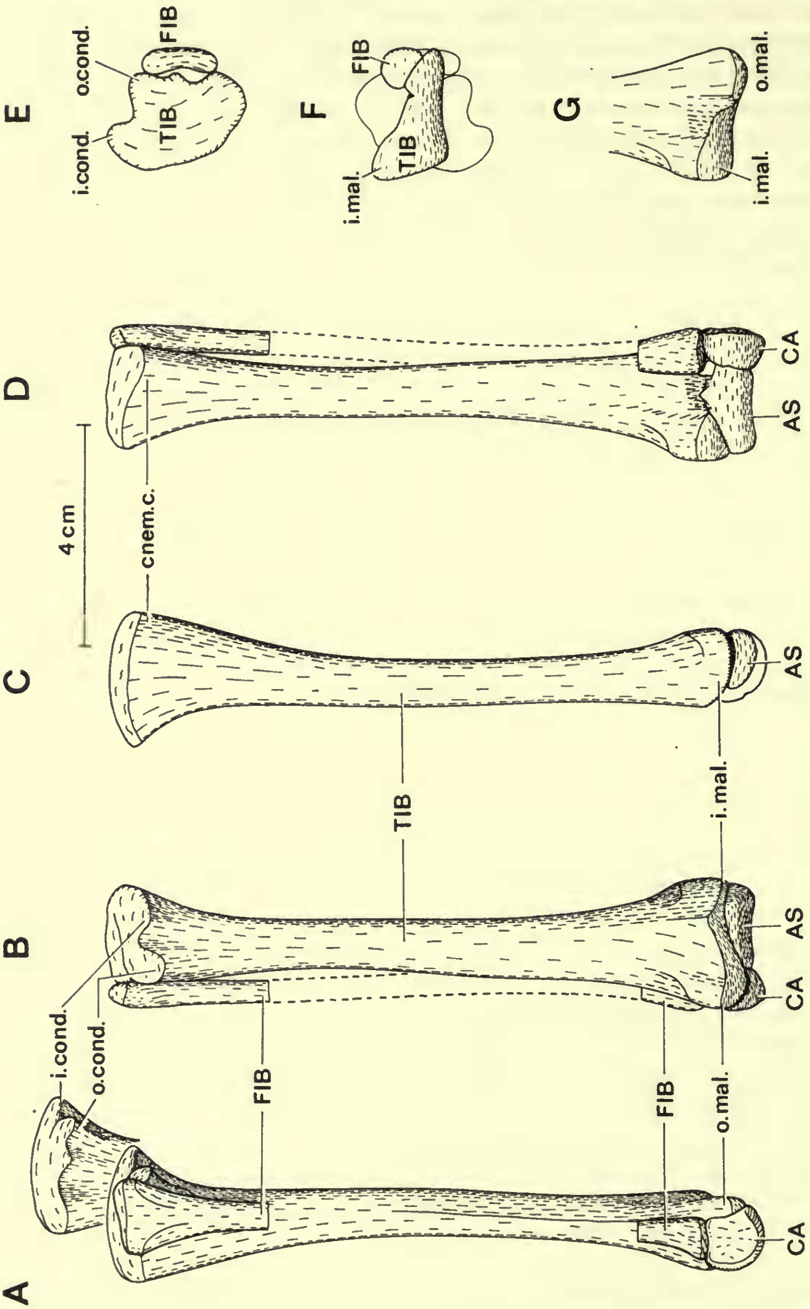

FIG. 56. *Hypsilophodon foxii.* Tibia, fibula, astragalus and calcaneum R5830, × $\frac{3}{4}$. A, lateral view; B, posterior view; C, medial view; D, anterior view; E, proximal view; F, distal view of tibia and fibula; G, anterior view of distal part of tibia. Abbreviations: AS, astragalus; CA, calcaneum; FIB, fibula; TIB, tibia; cnem. c., cnemial crest; i. cond., inner condyle; i. mal., inner malleolus; o. cond., outer condyle; o. mal., outer malleolus.

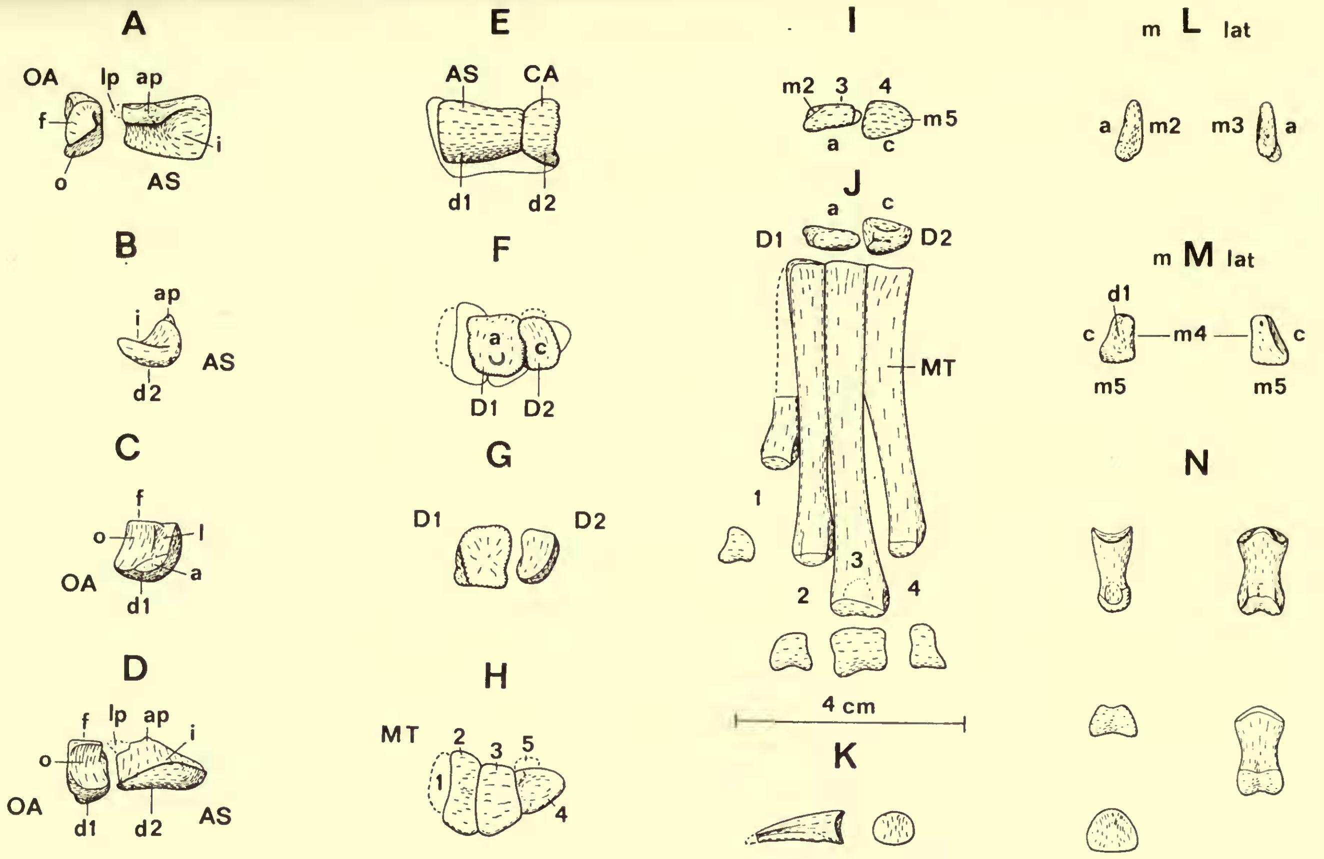

FIG. 57. *Hypsilophodon foxii.* R5830, × $\frac{3}{4}$. A, astragalus and calcaneum, proximal view; B, astragalus, lateral view; C, calcaneum, medial view; D, astragalus and calcaneum, posterior view; E, astragalus and calcaneum, distal view; F, distal tarsals, proximal view of metatarsus; G, distal tarsals, distal view; H, metatarsus, proximal view; I, distal tarsals, ventral view; J, distal tarsals and metatarsus, dorsal view with distal view of metatarsals I to IV; K, ungual phalanx, lateral and proximal views; L, distal tarsal 1, medial and lateral views; M, distal tarsal 2, medial and lateral views; N, phalanx, lateral, dorsal, distal, ventral and proximal views. Abbreviations: AS, astragalus; CA, calcaneum; D, distal tarsal; MT, metatarsal; a, surface for astragalus; ap., anterior ascending process; c, surface for calcaneum; d, surface for distal tarsal; f, surface for fibula; i or im, surface for inner malleolus; l, surface for lateral process; lp., lateral process; m, surface for metatarsal; o, surface for outer malleolus.

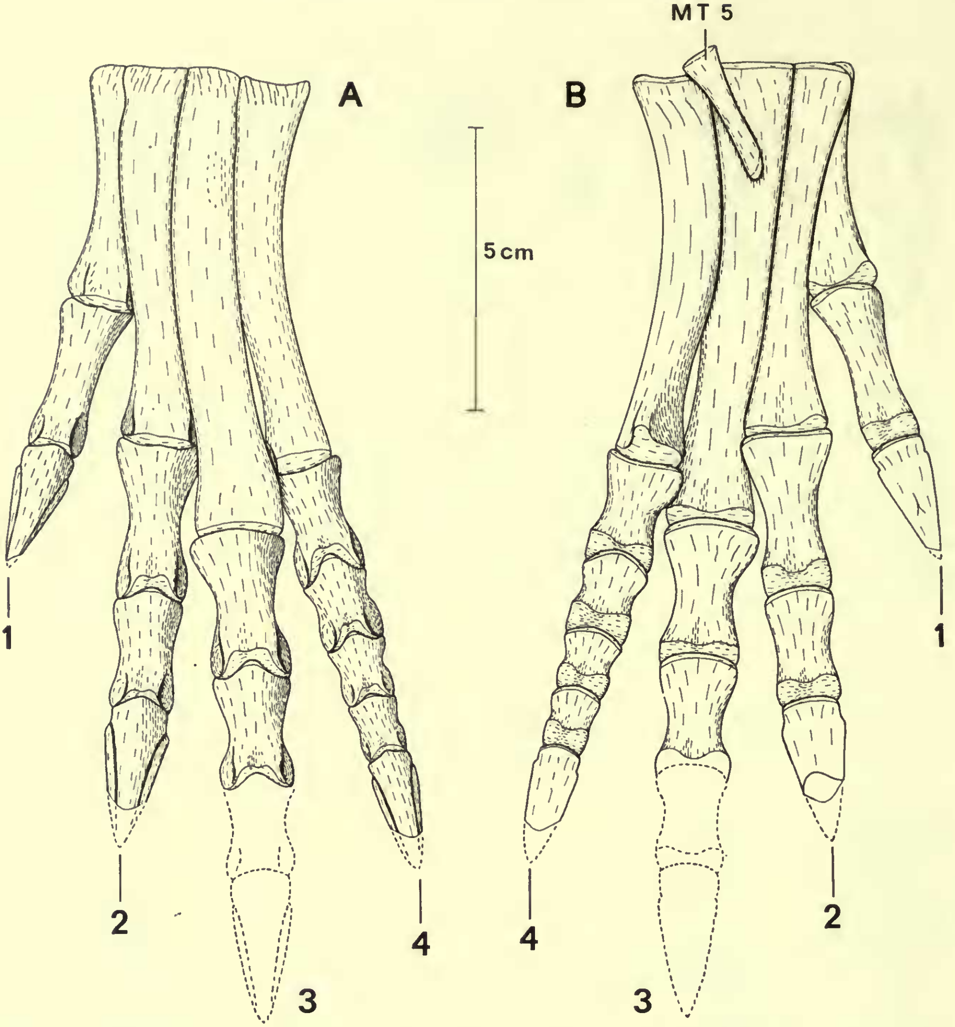

Fig. 58. *Hypsilophodon foxii.* Pes R196, × ¾. A, dorsal view; B, ventral view with details of metatarsal V from SM 4127. Abbreviations: MT, metatarsal; 1–5, digits.

region in the ventral half. Most of the distal surface (Text-fig. 57G) is flat with radiating surface markings; the proximal end of metatarsal III articulated with the lateral two-thirds of this surface. The ventro-medial corner is bevelled to form a distinct depression (Text-fig. 57G). A well-developed boss on metatarsal II (Text-fig. 57H) fitted into this depression while the remainder of the lateral part articulated with the flat surface of this distal tarsal (cf. Text-figs. 57G, H).

Distal tarsal 2. This is a rather irregular wedge-shaped bone. The proximal (Text-fig. 57F) and distal surfaces (Text-fig. 57G) are concave. The inner surface (d.1 Text-fig. 57M) is markedly concave and fitted against the lateral surface of distal tarsal 1. This depression continues a short distance on to the dorsal surface (Text-fig. 57J). The outer and ventral surface (Text-fig. 57J) form a continuous and obliquely inclined curve progressively increasing with width (Text-fig. 57M). The reduced fifth metatarsal articulated with the wide ventral part of this surface.

Metatarsals. The relative length of the metatarsals varies, but metatarsal III is always the longest and stoutest with metatarsal I about half as long. In R5830 metatarsals II and IV are approximately equal but in all other specimens metatarsal II is slightly shorter than metatarsal IV. The anterior (dorsal) surface of the metatarsus is transversely convex (Text-figs. 57H, 58A) with well-marked corners which become more rounded distally. Proximally the metatarsals are expanded antero-posteriorly with the anterior face sweeping upwards so that a deep articular surface is formed, especially large in metatarsals II and III (Text-fig. 57H). The posterior surface of the metatarsus is concave (Text-figs. 57H, 58B), although the individual metatarsals are gently convex and becoming more strongly curved distally.

The distal articular condyle of metatarsal I is not reduced (Text-figs. 57J, 58) and the adjacent part of the shaft is subtriangular in cross-section. The shaft becomes more compressed so that the proximal part is thin and flat with almost no proximal articular surface. The amount of the first metatarsal visible in ventral view (Text-fig. 58B) progressively decreases because the flattened proximal part wraps round on to the dorso-lateral surface of the second metatarsal (Text-fig. 58A). The proximal end of metatarsal II is bioconcave with a well-developed bump towards its rear surface (Text-fig. 57H) which fitted against the step on distal tarsal 1. The medial surface is rounded beyond the end of metatarsal I, while the flat lateral surface against metatarsal III is reduced distally so that the shaft becomes almost circular in section. The proximal end of metatarsal III has an irregular surface which fitted against distal tarsal 2. The cross-section of the shaft near the distal end is a dorso-ventrally flattened circle. The proximal end of metatarsal IV is concave, with a well-developed bump on each of the inner corners (Text-fig. 57H), and it contacted distal tarsal 2. Most of the shaft is somewhat triangular in outline with a sharp lateral edge formed by the junction of the gently convex anterior and posterior surfaces. The distal half diverges laterally and also slightly posteriorly from metatarsal III. In ventral view (Text-fig. 58B) there is an edge on the medial margin which gradually passes laterally until it merges with the roots of the outer condyle. The shaft internal to this ridge is convex but external to it is gently concave. This ridge is also well developed in R200 and S.M. 4127 but it is absent in R5830 ; its development is probably related to size. Metatarsal V is reduced to a splint which is well preserved in S.M. 4127 (basis for Text-fig. 58B). The proximal end is transversely expanded to form a head, oval in section and with a rounded end which articulated with the posterior surface of distal tarsal 2. The distal end has an obliquely inclined articular surface but no phalange was found.

Phalanges. The proximal ends of the first and last phalanges of each digit do not bear a well-developed dorsal process as do the other phalanges (Text-fig. 58A). These processes appear to be less strongly developed in R5830 than they are in R196 ; this is probably due to the difference in size. The proximal ends (Text-fig. 57N) are concave with a median ridge so that two depressions are formed. These are shallow in the first and ungual phalanges (Text-fig. 57K) but are well developed in the others. The lateral muscle grooves are well developed on the distal condylar head (Text-fig. 57N). The central depression is continued dorsally on to the non-articular part and the resulting cavity received the dorsal process of the next phalanx. The ungual phalanges are slender (Text-figs. 57K, 58) and the grooves for the claw are well developed.

e) *Dermal armour*

A few thin sheets of bone are present close to the skull of specimen R2477. Hulke (1874, pl. 3, fig. 1) figured these and regarded them as thin scutes, noting that they were 'irregularly polygonal' in outline with one surface granular, the other smooth and furrowed by a vascular net. In a later paper (1882) they were figured but neither labelled nor mentioned. Nopcsa (1905, fig. 4) figured them and noted (: 205) that *Hypsilophodon* was 'clad with a thin but well developed dermal armour consisting of comparatively large yet thin and flat, feebly punctured plates'. He also noted that they showed the same feebly grooved sculpture and could not be referred to any part of the endoskeleton. Romer (1956 : 428) noted that '*Hypsilophodon* had a paired row of thin dorsal plates presumably retained from the thecodont ancestors'.

The thin overlapping plates of bone were shown by Nopcsa (1905, fig. 4) but it is impossible to determine their original shape as all the edges are broken. The plates lie lateral to the distal parts of the dorsal ribs of individual 'a' and very close to a skull that probably belongs to another individual (Hulke 1874, pl. 3, fig. 1, 2 ; Galton 1967, photograph fig. 23). However, it is not certain to which individual the plates belong. Consequently there is no evidence to show that the plates were paired or dorsal in position. Both surfaces are rough, lacking the smooth finish of other bones, with various small and irregularly shaped depressions.

It is possible that these plates formed part of a dermal armour. However, if such were the case it is surprising that they have not been preserved in any of the other specimens. In R194 there is a similar plate, about a square inch in size, but it is so eroded that it could be anything. It is particularly surprising that these elements were not preserved in R196 because this skeleton is so complete in all other respects. Nopcsa (1905) could not identify these plates as any part of the endoskeleton but they could be the remains of a damaged sternum. Consequently, although they may well represent dermal armour, further material is needed to confirm this identification. Dermal armour is present in most thecondontians but *Hypsilophodon* is the only ornithopod in which dermal armour has been reported. In stegosaurs and ankylosaurs dermal plates formed a strong armour.

V. *CAMPTOSAURUS VALDENSIS*–A LARGE *HYPSILOPHODON FOXII*

Lydekker (1888) noted that the damaged left femur R167 (Pl. 2, fig. 4) might, because of its greater size, represent a species distinct from *Hypsilophodon foxii*. He also catalogued a small mandibular ramus R180 as that of a young *Iguanodon* (Owen 1864, pl. X figured it as this). In the same year he stated (1888*a*) that this ramus might belong to a smaller adult form, allied to *Laosaurus* or *Dryosaurus*, in which case the femur R167 might belong to the same form. Subsequently (1889) he noted that the femur was very similar to that of *Camptosaurus leedsi* from the Oxford Clay, which is itself very similar to the femur of the North American *Camptosaurus*. Because there was no other evidence of a *Hypsilophodon* of these dimensions he made the femur R167 the type of a new species, *Camptosaurus valdensis*, to which he provisionally referred the mandibular ramus. He listed the femur and jaw as *Camptosaurus valdensis* in the supplement to his catalogue (1890).

Gilmore (1909) noted that the fourth trochanter of R167 was on the proximal half of the shaft and he opined that, because in the American *Camptosaurus* it is on the distal half, this femur must be distinct from *Camptosaurus*. There are other differences between the two. The lesser trochanter of R167 is not expanded anteroposteriorly and the cleft separating it from the greater trochanter is shallow and ends level with the middle of the head. In the American *Camptosaurus* (Gilmore 1909, fig. 42–1) and *C. leedsi* (Lydekker 1889, fig. 3) the trochanter is expanded and the cleft is deep and ends level with the bottom of the head. In addition, *Camptosaurus* has a well-developed anterior intercondylar groove which is absent in R167.

In the characters cited (the position of the fourth trochanter, the shape of the lesser trochanter, the depth of the cleft between the lesser and greater trochanters and the absence of a marked anterior intercondylar groove) the femur R167 agrees with those of *Hypsilophodon* (Text-figs. 54, 55). Consequently this femur is regarded as belonging to the genus *Hypsilophodon*.

Lydekker (1888, 1889) emphasized the large size of the femur R167 in comparison with those of *Hypsilophodon foxii*; Swinton (1936*b*) stated that it is half as large again as any femur known in that genus. The total length of R167 is unknown but the minimum distance between the proximal end and the distal surface of the fourth trochanter is 108 mm (see Text-fig. 1f). The distance in R5829 (the largest femur generally regarded as *Hypsilophodon foxii*) is 87 mm, so R167 is not quite 25 per cent as large again. The femur of R167 is therefore regarded, not as representing a new species but, on the contrary, as a femur of *Hypsilophodon foxii* from the largest individual hitherto found, which would have been about 7·5 ft or 2·28 m long.

The teeth of the mandibular ramus (R180) mentioned above resemble the corresponding teeth of *Iguanodon atherfieldensis* (see Hooley 1925). Therefore this ramus is referred to a young *Iguanodon*, following Owen (1864) and Lydekker (1888). This was the only other specimen referred to *Camptosaurus valdensis*; consequently the genus *Camptosaurus* is not so far represented in the Wealden of the Isle of Wight.

VI. ASPECTS OF CRANIAL ANATOMY

a) *The foramina of the braincase*

The foramina for the *olfactory*, *optic* and *trochlear nerves* (I, II and IV) are not preserved because the more anterior part of the braincase was cartilaginous. The same is true of the dorsal boundary of the large foramen for the oculomotor nerve III. The dorsal edge of the parasphenoid is concave and probably formed the ventral border to this foramen (III, Text-fig. 60A). The resulting foramen bears exactly the same relationship to the surrounding structures as does the foramen for the oculomotor in hadrosaurs (see Ostrom 1961, fig. 12).

Trigeminal foramen (V, Text-figs. 4B, 9, 60A). This large foramen is enclosed mainly by the prootic but anteriorly it is bordered by the laterosphenoid. On the lateral surface of the laterosphenoid there is a short groove which passes antero-dorsally from the trigeminal foramen (Text-figs. 9A, 60A). The deep ophthalmic ramus (V_1), a sensory tract from the snout that branches off close to the braincase, probably ran in this groove. In hadrosaurs there is another groove running ventrally for the maxillary and mandibular rami (V_2 and V_3) ; in *Hypsilophodon* there is no well-developed groove but the common course of these two rami is faintly discernible, probably passing postero-ventrally to the edge of the step running from the base of the basipterygoid process (Text-figs. 4B, 60A). There is a slight depression on the posterior face of this edge which was probably for those two rami. The maxillary ramus (V_2) presumably passed forwards above the base of the pterygoid process while the mandibular ramus (V_3) continued ventrally ; these routes are visible in hadrosaurs (Ostrom 1961) but not in *Hypsilophodon.*

Abducent nerve (VI). The abducent of hadrosaurs arises from the floor of the metencephalon and passes through bone in a long canal, part of which is lateral to the sella turcica, to emerge through the oculomotor foramen (Ostrom 1961). The position appears to be the same in *Hypsilophodon* but the part in the lateral wall of the sella turcica is not enclosed by bone. The exit of a canal into this part of the sella turcica is visible on both sides in R2477 but its entrance into the inner wall of the braincase cannot be located.

Facial nerve (VII) passes through a small foramen in the prootic (Text-figs. 9, 60A). Leading ventrally from this there is a groove which continues ventrally medial to the groove already mentioned for V_2 and V_3. The anterior branch (palatine ramus) of the facial nerve presumably ran in this groove and then passed ventral to the basipterygoid process.

In medial view (Text-figs. 9B, C) the posterior part of the prootic of *Hypsilophodon* shows a process which meets a corresponding process of the opisthotic. The anterior opening bounded by the prootic was probably for the *auditory nerve* (VIII). The posterior opening bounded by the opisthotic is interpreted as a combined *foramen lacerum posterius* (for cranial nerves IX, X and XI) and *jugular foramen* (for the internal jugular vein). This common opening is separated from the *internal auditory meatus,* the *inner ear cavity* and the *fenestra ovalis* by a thin bony partition (Text-fig. 9A). A similar partition is mentioned by Gilmore (1914) in *Stegosaurus.* Medially (Text-fig. 9C) the three cranial nerves share a single opening but more laterally there is a small tunnel in the posterior wall which forms a separate exit visible in lateral view (Text-fig. 9A). This posterior opening was probably for the *accessory nerve* (XI) while the *glossopharyngeal* (IX) and *vagus* (X) nerves remained in the main foramen. In hadrosaurs the foramen for the accessory nerve is completely separate from the other two (Ostrom 1961). The foramen for the *hypoglossal* nerve (XII) is completely enclosed by the opisthotic (Text-figs. 9A, C).

In medial view (Text-figs. 9B, C) there are three features of the braincase which are not associated with cranial nerves : the fossa subarcuata, the lagenar recess and the opening for the vena cerebralis posterior. The sutural region between the supraoccipital and the prootic is excavated to form a large and tapering tunnel. A similar structure is present in *Plateosaurus*, interpreted by Janensch (1936, fig. 3) as the *fossa subarcuata*. The structure of the middle ear of *Hypsilophodon* cannot be determined but was probably similar to that of hadrosaurs as described by Ostrom (1961). In *Hypsilophodon* only part of the *lagenar recess* is visible ; this forms a concave depression on the postero-ventral part of the prootic ventral to the fenestra ovalis. On the opisthotic immediately above the medial opening of the hypoglossal nerve there is an opening (f, Text-figs. 9B, C) which leads into a small tunnel. Janensch (1955) labelled a similar opening in *Dysalotosaurus* as the vena cerebralis posterior ; he had discussed this identification in an earlier paper (1936).

b) *The paroccipital process and the post-temporal fenestra*

What appears to be part of the suture between the exoccipital and the opisthotic is visible on the medial surface of R8418 (Text-fig. 9B). The suture forms a clearly defined edge which, because the bone surface is well formed with faint markings, is not the result of displacement along a crack. Consequently it appears that in *Hypsilophodon* the exoccipital portion is restricted to the lateral part of the occipital condyles. The part through which the foramina pass is part of the opisthotic as is the paroccipital process.

Langston (1960) described a fragmentary skull of a hadrosaur in which the main occipital part of the paroccipital process appeared to be formed by the exoccipital. Overlapping this anteriorly but not extending to its distal end was a smaller process formed by the opisthotic. The tapering part of the prootic overlapped the base of the opisthotic anteriorly. However, the form of the paroccipital process was quite normal and it should be noted that several of the suture lines are shown dotted. Langston stated that in camptosaurs the opisthotic does not form part of the paroccipital process. Regarding the position in *Camptosaurus* Gilmore (1909 : 207) stated that 'the exoccipital and opisthotic are firmly coalesced, and there is no indication of the position of the suture that evidently was early obliterated'. He regarded the portion forming the occipital condyle as exoccipital and the rest, including the paroccipital process, as opisthotic. Janensch (1955) considered that in the hypsilophodont *Dysalotosaurus* all the bone behind the prootic was exoccipital with no mention of the opisthotic. Information from other specimens is needed to ascertain whether the paroccipital process of ornithischians is usually formed by the opisthotic or by the exoccipital.

In hadrosaurs the very small post-temporal fossa is bordered ventrally by the paroccipital process (see Langston 1960) while in *Hypsilophodon* it is totally enclosed by the paroccipital process (Text-figs. 7B, 8, 9B). Leading antero-medially and dorsally from the resulting foramen is a slight depression which soon disappears. However, more anteriorly on the side of the supraoccipital there is a well-defined groove which passes medial to the parietal to enter the braincase (Text-fig. 60A).

The anterior groove and the posterior depression are in line, bearing the same relationship to the edge of the supraoccipital, so it is reasonable to conclude that the same structure occupied both. The resulting course rules out a nerve so this structure must have been a blood vessel, presumably the vena capitis dorsalis. Cox (1959) pointed out that in *Sphenodon* (O'Donoghue 1929) and *Lacerta* (Bruner 1907) the vena capitis dorsalis, which drains the muscles of the spino-occipital region, runs anteriorly through the post-temporal opening. Just before it enters the braincase it receives an anterior factor, the sinus-like vena parietalis, from above the parietal bone. In *Lacerta* the vena capitis dorsalis passes through the posterior end of the great parietal fissure (between the parietal and the prootic) to join the vena cerebralis media (Bruner 1907). In *Hypsilophodon* the route is similar though it is between the parietal and the supraoccipital. On the parietal there is a slight depression, running antero-dorsally from the projection on the ventral edge (Text-fig. 60A), which was probably for the vena parietalis. Consequently a vena capitis dorsalis ran along the lateral surface of the supraoccipital and the paroccipital process of *Hypsilophodon*. The presence of this vessel confirms the identification of the foramen in the paroccipital process as the remnant of the post-temporal fossa.

c) *The eye*

The orbit of *Hypsilophodon* (Text-fig. 3) is large and the interorbital septum, which was presumably present, was very high. As reconstructed the sclerotic ring is also large though, as noted above, it may have been slightly smaller than shown. The orbital surfaces of the prefrontal, frontal, postorbital and jugal are all inclined rather obliquely (Text-figs. 4A, 5A, 6B). In addition the dorsal edge formed by the prefrontal, frontal and postorbital is cut back, forming a sharp and well-defined edge to the orbit. All these features indicate that the eye of *Hypsilophodon* was large and filled the orbit as in birds.

In dorsal view (Text-fig. 5B) the striking features about the skull are the largeness of the orbits and the narrowness of the frontals. The eye of *Hypsilophodon* would have projected slightly and this is confirmed by the shape of the supraorbital that curves out laterally. The rather oblique configuration of the orbit in dorsal view (Text-fig. 5B) suggests that the fields of view overlapped slightly when the eyes looked more anteriorly. Certainly in anterior view (Text-fig. 7A) much of the posterior part of the orbit is visible.

In *Hypsilophodon* the sclerotic ring is only slightly convex in transverse section. Underwood (1970) notes that this form indicates that there was a sharp change of curvature between the posterior and anterior segments of the eye, with a well-developed sulcus, indicating good powers of accommodation and diurnal habits. Underwood also states that the diameter of the inner and outer edge of the ring gives an indication of the relative size of the cornea. An inner diameter of about a third or less of the outer is a fair indication of diurnal habits. This cannot be accurately applied to the ring of *Hypsilophodon* because the reconstruction is rather tentative with regards to these measurements. However, it seems likely that *Hypsilophodon* had quite good powers of accommodation and was diurnal in its habits.

The form of the orbit might suggest that *Hypsilophodon* was arboreal but, as discussed below, *Hypsilophodon* was not specifically adapted for tree-climbing and was probably cursorial. *Heterodontosaurus* (Crompton & Charig 1962), *Parksosaurus* (Parks 1926, Galton in press) and *Dysalotosaurus* (Janensch 1955) are other ornithopods with large orbits and these, as shown by the proportions of their hindlimbs, were probably also fast runners. Outside the Ornithischia the closest approach to the relative largeness of the orbits is in *Ornithomimus* (see Romer 1956, fig. 81A), a definitely cursorial animal.

The function of the sclerotic ring must be considered. Edinger (1929) showed by experiments on the lizard *Ophisaurus* that the plates do not change their relative position and, consequently, do not aid in the dilation of the pupil as has been suggested. However, they must aid in supporting and maintaining the shape of the eyeball. Ostrom (1961) considered it unlikely that this was their function because forms with sclerotic rings occupy an extremely wide range of habitats and, in addition, related forms without rings may occupy the same habitat as forms with them. He therefore concluded that the function of these structures has not yet been determined. Colbert (1962) noted that the function of the sclerotic ring was debatable. However, Walls (1942) discussed the function of the sclerotic ring as follows. The typical sauropsid sclera consists mainly of a cartilaginous cup of which the open rim extends quite close to the edge of the cornea. The remaining zone of the sclera is occupied by the sclerotic plates which are lacking only in crocodilians and snakes. Because the plates are flat or concave they do not continue the rotundity of the equatorial sclera smoothly into the sharper curve of the cornea. On the contrary the sclero-corneal junction is depressed or concave to form a broad annular sulcus. Walls (1942 : 275) stated that 'the production of a sulcus is the whole meaning, physiologically, of the sauropsidan ossicular ring. It stiffens the concavity against the force of the intraocular pressure which, if unresisted, would evaginate it. This pressure rises slightly during accommodation, which it does not do in fishes, amphibians or mammals.' He noted that the presence of a sclero-corneal sulcus resulted in the ciliary body touching the lens. The striated ciliary muscles are arranged in such a way that they cause the ciliary process to squeeze the lens so that its anterior surface becomes more rounded (for figures showing the mechanism of accommodation in the eyes of reptiles and birds see also Young 1962, figs. 218, 293).

The sclerotic ring is absent in crocodiles, snakes and mammals. Walls (1942) suggested that the loss of the sclerotic ring in modern crocodiles can be attributed to the adoption of nocturnal habits in which the images are crude and accommodation useless. The eye of snakes, when compared with that of lizards (see Young 1962, fig. 238), shows that many structures have been lost and that there are various improvisations to give the same results. Walls (1942) suggested that a burrowing mode of life in the ancestral snake led to the loss of many structures in the eye so that when snakes subsequently came above ground they had to adapt what was left. This theory has been disputed but a phase of nocturnal existence would be adequate to explain the loss of the sclerotic ring. In mammals accommodation relies on the elasticity of the lens capsule to supply the actual force of accommodation. Walls

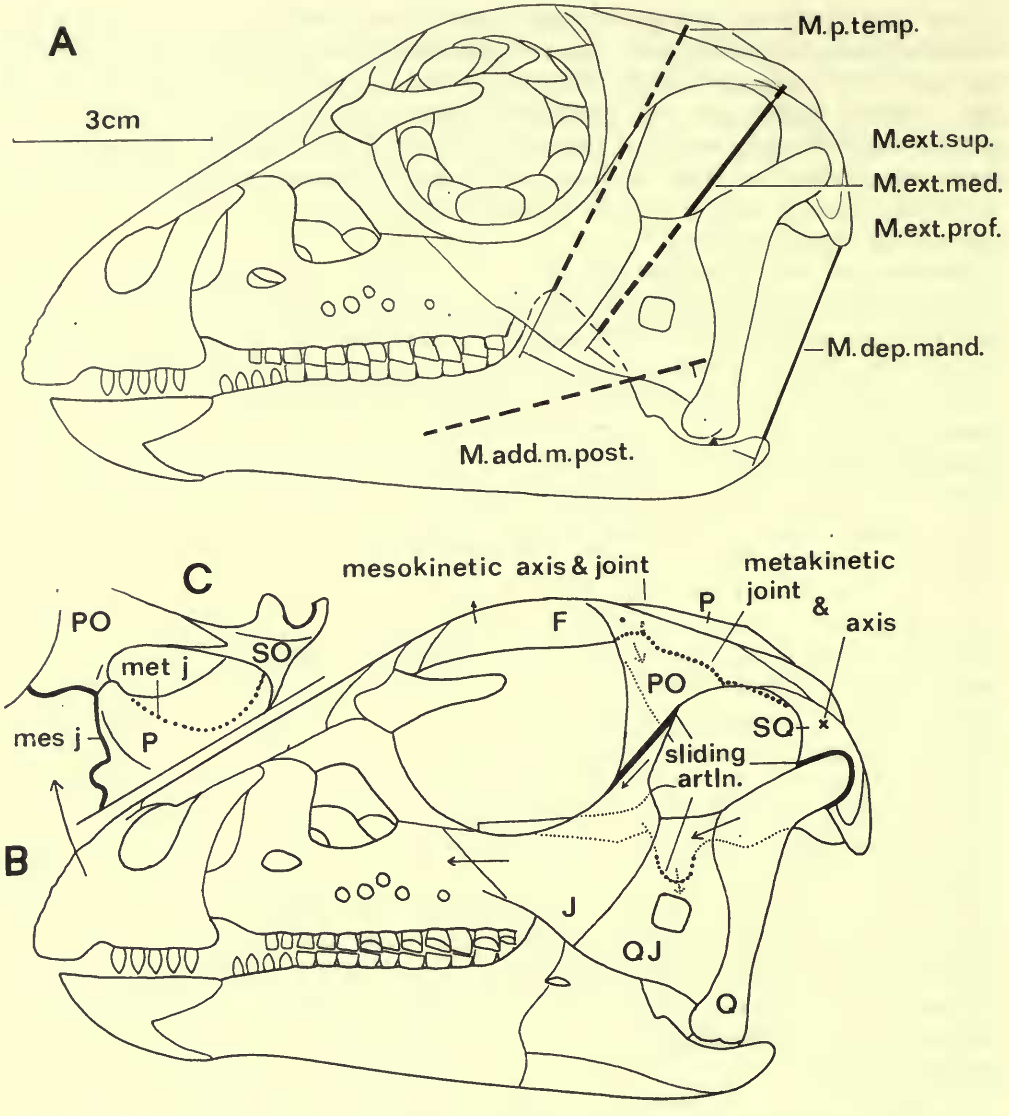

FIG. 59. *Hypsilophodon foxii.* Skull R2477, × 1. A, the lines of action and moment arms of the jaw muscles. Abbreviations for the muscles in Text-figs. 59A and 60 :

M. add. m. post.	M. adductor mandibulae posterior
M. dep. mand.	M. depressor mandibulae
M. ext. med.	M. adductor externus medialis
M. ext. prof.	M. adductor externus profundus
M ext. sup.	M. adductor externus superficialis

M. prot. pt.	M. protractor pterygoidei
M. pt. dor.	M. pterygoideius dorsalis
M. p. temp.	M. pseudotemporalis
M. pt. vent.	M. pterygoideus ventralis
Pt. D.	M. pterygoideus D (anterior division of M. pt. dor.)
Pt. V.	M. pterygoideus V (anterior division of M. pt. vent.)

B, the regions of movement in the skull, lateral view ; for discussion see page 110 ; C, the regions of movement in the skull roof. Abbreviations : mes j, mesokinetic joint ; met j, metakinetic joint ; sliding artln., sliding articulations. For abbreviation of skull bones see page 109.

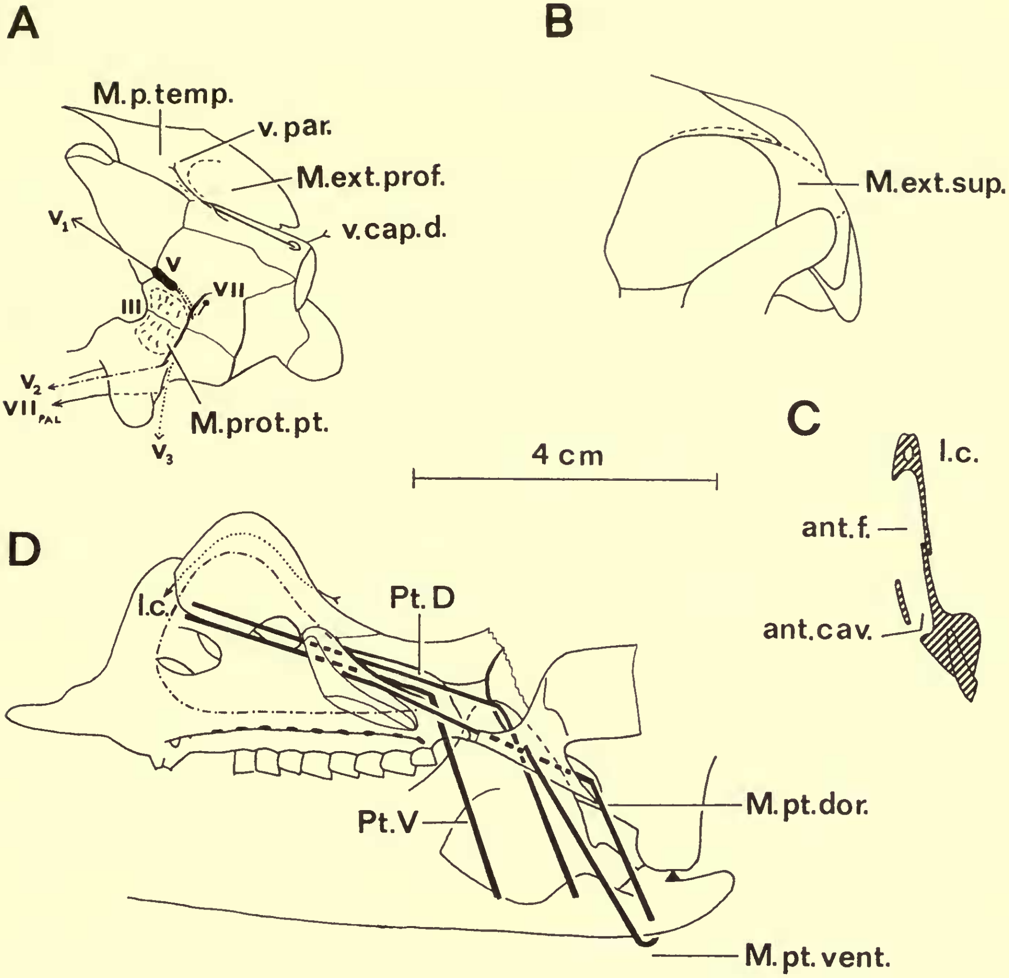

FIG. 60. *Hypsilophodon foxii.* Details of the skull R2477, × 1. A, braincase in lateral view to show areas of muscle attachment and routes of nerves and blood vessels, compare with Text-fig. 4B; B, area of origin of M. adductor externus superficialis, compare with Text-figs. 3, 4A; C, vertical section through the lachrymal and maxilla taken along line below middle of lachrymal; D, medial view to show lines of action of pterygoideus musculature, compare with Text-figs. 5A, 10B and Pl. 2, fig. 2. Abbreviations: ant. cav., antorbital cavity or fossa; ant. f., antorbital fenestra; l.c., lachrymal canal; v, cap. d., vena capitis dorsalis; v. par., vena parietalis; III, oculomotor foramen; V, trigeminal nerve; V_1, ramus ophthalmicus; V_2, ramus maxillaris; V_3, ramus mandibularis; VII, facialis nerve; VII_{pal} ramus palatinus. For abbreviations of muscles see page 108.

(1942) noted that mammals originated from forms with small bodies which were almost certainly nocturnal.

It is apparent that the sclerotic ring of dinosaurs, as in other sauropsids, was essential for accommodation because it maintained the shape of the sulcus. The absence of the ring in animals occupying the same terrestrial habit as others with it can be explained by a nocturnal phase in the ancestry of the former.

d) *Jaw musculature*

Apart from the cranial crests and specializations associated with the large dental batteries the hadrosaur skull is basically similar to that of *Hypsilophodon*. Ostrom (1961), who used about 80 skulls, gave a detailed account of their cranial musculature. By using this account in conjunction with the skull of R2477 a good idea of the jaw musculature of *Hypsilophodon* can be obtained. The inferred lines of action of the muscles are shown in Text-figs. 59, 60D. Ostrom (1961) followed the tripartite division of the mandibular musculature established by Luther (1914) and Lakjer (1926). These divisions are separated on their function and innervation rather than on their position. The adductor mandibulae group, which includes the superficial muscles of the temporal region, functions to close the jaws. Medial to this in forms with a kinetic skull is the constrictor dorsalis group which elevates the maxillary segment. The last group, the intermandibular muscles, aids in swallowing and respiration. The remaining muscle concerned with jaw movement is the M. depressor mandibulae – a branchial muscle which acts to open the lower jaw.

i) ADDUCTOR MANDIBULAE GROUP

The adductors are separated into external, internal and posterior masses according to their relationship with the branches of the trigeminal nerve (Luther 1914, Lakjer 1926 ; see Ostrom 1961 for details).

M. adductor mandibulae externus. This is the most variable of the adductor muscles in fishes, amphibians and reptiles and is typically divided into three parts : partes superficialis, medialis and profundus.

Pars superficialis. Origin : on the lateral surface of the squamosal of *Hypsilophodon*, anterior and dorsal to the head of the quadrate, there is a well-defined depression (Text-fig. 4A). This depression forms a sharp edge, slightly undercutting the flat dorsal surface (Text-fig. 5B) ; it is continued anteriorly on to the ventral edge of the postorbital as a bevel (Text-figs. 4A, 60B). However, Ostrom (1961, fig. 34) concluded that the very similar depression in hadrosaurs was for the pars superficialis, although the reptilian pars superficialis typically originates on the medial surface of the upper temporal arch and rarely develops a prominent scar. As Ostrom noted, the position and shape of the depression in hadrosaurs suggest that it is an extension of the lower temporal fenestra and is consequently a reflection of the superficial temporal muscle. Only a small area is involved and this would concentrate the stresses, resulting in the prominent scar (Ostrom 1961). Insertion : there are no well-defined insertion markings to indicate the area of insertion in

Hypsilophodon or hadrosaurs. However, it probably inserted on to the postero-dorsal edge of the surangular and to its medial surface. The more dorsal part of this edge near the coronoid is much thicker (Text-fig. 10B), the reverse of the position in hadrosaurs, but it lacks the well-defined and slightly concave dorsal surface present in hadrosaurs. The partes medialis and profundus probably inserted in the same region.

A more lateral subdivision of the superficialis, the *M. levator, anguli oris*, was possibly present on the ventral border of the jugal. Ostrom (1961) noted that this border in hadrosaurs and *Iguanodon* shows a pronounced ventral lobe which was possibly for this muscle. A similar lobe is well developed in *Protoceratops* and was probably for the same muscle (Haas 1955) as was the large lobe in *Heterondontosaurus* (see Crompton & Charig 1962, fig. 1B 'J.F.'). The anguli oris probably inserted in front of the coronoid and on the quadratomaxillary ligament (Ostrom 1961) or possibly on to the outer surface of the coronoid region.

Pars medialis. Origin : in modern reptiles this muscle is medial to the pars superficialis but occupies a similar position. In hadrosaurs there is a well-defined area for the pars medialis on the medial surface of the postorbital and the lateral process of the squamosal ; it is bounded posteriorly by a well-defined ridge on the squamosal (Ostrom 1961, fig. 36). This ridge is absent in *Hypsilophodon* but the area occupied by the medialis was probably the same.

Pars profundus. Origin : in modern Sauropsida this muscle fills most of the upper temporal fenestra. In hadrosaurs Ostrom (1961, fig. 38) located this origin chiefly on the parietal and squamosal next to the medialis. The anterior limit is defined by a gentle ridge running postero-dorsally across the side of the parietal. In *Hypsilophodon* the anterior limit is marked by the edge of a slight depression on the ventro-medial half of the parietal (Text-fig. 60A). Consequently the pars profundus probably originated from the ventro-medial part and the lateral wing of the parietal and, in addition, from the anterior surface of the medial process of the squamosal.

M. adductor mandibulae internus

M. pseudotemporalis. Origin : in modern reptiles the M. pseudotemporalis originates from the deep position in the anterior part of the upper temporal fenestra, passing anterior to the trigeminal foramen. The posterior limit of this muscle is formed by the area of the previous muscle. In *Hypsilophodon* the M. pseudotemporalis overlapped the M. externus profundus dorsally to originate from the median crest (Text-fig. 60A). More anteriorly a ridge sweeps laterally across the parietal on to the postorbital ; it is continued by the dorsal edge of the postorbital. The region delimited by this ridge (Text-fig. 5B) indicates the anterior limit of the M. pseudotemporalis. Insertion : Ostrom (1961) deduced that this muscle must have inserted on to the coronoid in hadrosaurs although there is no distinct scar on that element. In *Hypsilophodon* there are, in contrast, well-developed insertion markings for the M. pseudotemporalis on the lateral, dorsal and medial surfaces of the coronoid bone (Text-figs. 10, 12).

M. pterygoideus. This muscle, which is not homologous with the mammalian muscle of that name, is divided into two parts in modern reptiles and birds. In hadrosaurs Ostrom (1961, figs. 42, 43) placed the origin of the pars dorsalis on the well-developed maxillary shelf formed by the postero-medial part of the maxilla and by the ectopterygoid. In *Hypsilophodon* there is no equivalent shelf region on the maxilla but the dorso-medial surface of the ectopterygoid is similar to that of hadrosaurs. The *pars dorsalis* probably originated from the concave surface of the ectopterygoid. Posteriorly this surface is medially directed (Text-figs. 4B, 5C) but more anteriorly it is dorsally directed (Text-fig. 5C) because the surface is twisted along its length. There is no trace of the area of insertion but it was probably on the medial surface of the articular postero-ventral to the quadrate as in hadrosaurs (Ostrom 1961, fig. 41).

In hadrosaurs the *pars ventralis* probably originated from two depressions on the ventro-medial surface of the pterygoid (Ostrom 1961, fig. 42). In *Hypsilophodon* it probably originated from a corresponding flat surface formed by the pterygoid and ectopterygoid (Text-figs. 4B, 6A, 60D). This muscle wraps round the ventral border of the retroarticular process to insert on the lateral surface. In *Hypsilophodon* there is a slight depression on the region below the mandibular condyle in R192 which was probably for this muscle. In hadrosaurs there is a well-defined depression which corresponds in position to that of the pars dorsalis on the opposite side (Ostrom 1961, fig. 41). The areas of origin of the pars dorsalis and ventralis are discussed below in more detail in Section (g.)

M. adductor mandibulae posterior. In sauropsids this muscle originates in the postero-ventral corner of the temporal region and links the quadrate with the posterior part of the inframandibular fossa. In hadrosaurs the anterior surface of the quadrate shows a well-developed depression, extending on to the lower third of the pterygoid flange, which was the area of origin of the M. adductor posterior (Ostrom 1961, fig. 46). The area was presumably the same in *Hypsilophodon* though the depression is not visible on the pterygoid flange (Text-fig. 7B). The insertion in *Hypsilophodon* was clearly into the deep inframandibular fossa. This tapers anteriorly (Text-fig. 12A) and ends (apart from the Meckelian canal running forwards) level with tooth 7. The wall formed by the dentary bears well-developed insertion markings and this was evidently a powerful muscle.

ii) CONSTRICTOR DORSALIS GROUP

Three divisions of the constrictor dorsalis group are recognized by Lakjer (1926). Two of these, the M. protractor pterygoidei and M. levator pterygoidei, are concerned with movement of the dermal skull roof and palatoquadrate (maxillary segment) relative to the braincase (occipital segment). The third division, the M. levator bulbi, is concerned with movements of the eyelid. The first two muscles are absent in modern akinetic skulls such as those of Crocodilia, Chelonia and Mammalia.

Ostrom (1961) failed to find any evidence of insertion areas for the levator and protractor pterygoidei muscles in hadrosaurs but suggested that the M. levator bulbi was present. He noted (: 108) that 'anterior and ventral to the trigeminal foramen, located on the laterosphenoid between the bony grooves for the profundus and maxillary branches of the trigeminal nerve, is situated a moderately concave, antero-laterally facing, triangular surface which may have served as the origin site of the M. levator bulbi'. He stated that the position of this surface on the lateral wall of the braincase and the direction it faces, directly towards the orbit, supported this interpretation. Ostrom stated that the akinetic nature of the skull ruled out the possibility that this area was for either a levator or a protractor pterygoidei and that, in addition, no other site for the M. levator bulbi was found on any of the numerous skulls examined.

In *Hypsilophodon* there is an equivalent slightly concave surface, with insertion markings, which bears the same relationships to the profundus (V_1) and maxillary branches (V_2) of the trigeminal nerve (Text-figs. 4B, 60A) but, in contrast, it is on the prootic and basisphenoid. In hadrosaurs there are no sutures in this region so this surface could also be on the prootic and basisphenoid. It is considered likely that the concave surface in hadrosaurs is the same as that in *Hypsilophodon*.

Oelrich (1956) gave a detailed account of the anatomy of the skull of the lizard *Ctenosaura*. He showed a concave surface on the prootic and basisphenoid, immediately below the trigeminal foramen. This surface bears exactly the same relationship to the surrounding bones and nerves as that on the same bones in *Hypsilophodon* (compare Text-fig. 4B with Oelrich 1956, fig. 8). In fig. 53 Oelrich shows a muscle which clearly originates from this surface but it is not labelled. However, a comparison with fig. 35 shows that this is the M. protractor pterygoidei. Oelrich (1956 : 45) stated that the M. protractor pterygoidei 'forms the lateral wall of the tympanic cavity. It is a large fan-shaped muscle arising from the lateral surface of the anterior inferior process of the prootic, the lateral surface of the alar process of the basisphenoid, and the posterior border of a tendon which extends from the proximal end of the pila antotica to the cartilage covering the anterior tip of the basipterygoid process just above the condyle'. This suggests that the surface on the prootic and basisphenoid of *Hypsilophodon* could have been for the M. protractor pterygoidei. However, the relationship of this surface to the branches of the trigeminal nerve clearly shows that it is the same as that in hadrosaurs which, as Ostrom (1961) suggests, may have been for the M. levator bulbi. This possible difference may be related to differences of kinetism. The skull of *Ctenosaura* is kinetic with the M. protractor pterygoidei moving the ventral part of the braincase away from the parietal. Presumably this was the position in the kinetic ancestor of hadrosaurs. When the skull became akinetic the M. protractor pterygoidei was lost. In *Ctenosaura* (Oelrich 1956, figs. 7, 8, 35) the M. levator bulbi originates from the pila antotica which passes anteriorly from the area of origin of the M. protractor pterygoidei. If the situation was similar in the ancestor of hadrosaurs the M. levator bulbi had only to shift slightly posteriorly to occupy the surface originally occupied by the M. protractor pterygoidei. In *Ctenosaura* this surface faces antero-laterally directly towards the orbit and would provide an excellent surface for the M. levator bulbi. However, the surface in hadrosaurs may have been occupied by a M. protractor pterygoidei which formed the lateral wall of the tympanic cavity.

It is rather difficult to determine the composition of the constrictor dorsalis group in *Hypsilophodon*. If the skull was metakinetic then the group must have been as in *Ctenosaura* with the M. protractor pterygoidei on the prootic and basisphenoid and the M. levator bulbi on the more anterior pila antotica. In this case the M. levator pterygoidei would have originated from the parietal but there is no trace of such an origin in *Hypsilophodon.* However, this is hardly surprising because this muscle would have been only a slip and unlikely to leave any trace. If the skull of *Hypsilophodon* was akinetic then the position could still have been as in *Ctenosaura* with the lateral wall of the tympanic cavity formed by the M. protractor pterygoidei. The M. levator bulbi may have originated from the area on the prootic and basisphenoid previously occupied by the M. protractor pterygoidei but, as discussed in the next section, there are certain features which indicate that the skull might have been kinetic.

iii) CONSTRICTOR VENTRALIS GROUP

These muscles are thin sheets which link the two mandibular rami. Ostrom (1961) figured one specimen which shows a possible area of origin of the M. mylohyoideus but concluded that the position was indeterminable ; the same is true for *Hypsilophodon.*

iv) M. DEPRESSOR MANDIBULAE

As in all reptiles this branchial muscle linked the retroarticular process of the mandible to the dorsal occipital surface of the skull. In hadrosaurs there is an insertion area on the medial surface of the retroarticular process (Ostrom 1961) but its position cannot be determined in *Hypsilophodon.* Ostrom concluded that in hadrosaurs the depressor fibres originated from the tip of the paroccipital process, the form of which was probably determined by the stresses imposed by this muscle. This was presumably the case in *Hypsilophodon* also (Text-fig. 59A).

e) *Kinetism*

Versluys (1910) introduced the concept of kinetism with respect to the reptilian skull. A kinetic skull is one in which there is a movable joint between two segments of the braincase (neurocranium and/or dermal roofing bones). Frazetta (1962) recognized three types which are distinguished by the position of the hinge region. In prokinesis the hinge is between the nasal and frontal bones, in mesokinesis it is between the frontals and parietal, while in metakinesis it is between the parietal and supraoccipital (or other bones of the occipital series). A kinetic skull may have one joint (monokinetic) or two (amphikinetic). In addition there may be movement between individual parts of the maxillary segments (dermal skull roof and palatoquadrate).

In *Hypsilophodon* the nasals are overlapped by the frontals while the lateral part of this sutural region is overlapped by the dorsal sheet of the prefrontal (Text-figs. 5B, 6B) so it is unlikely that there was any movement in this region. The suture between the frontals and the parietal consists of a well-developed set of interdigitating ridges and grooves (Text-fig. 7B). At first sight it would appear that this suture was immobile but it is comparable to the frontoparietal suture of a large skull of *Varanus* at which movement occurred (Frazetta 1962). The presence of a good sutural system and a slight hinging action are not necessarily incompatible because the former compensates for any weakness resulting from the latter. The frontal of *Hypsilophodon* has a laterally directed spike which is enclosed by the postorbital (Text-figs. 4B, 7B, 8). The postorbital probably remained fixed in position with respect to the parietal because there is a suture between them and because it received the head of the laterosphenoid ventrally (Text-fig. 6B). In addition the postorbital overlaps the squamosal with which it forms the temporal bar. As the pars superficialis, the pars medius and part of the pars profundus of the M. adductor mandibulae externus originated on this bar it is unlikely that there was any movement between its two parts. A slight hinging may have occurred at the fronto-parietal suture (mesokinetic joint) with the mesokinetic axis on the line across the frontals joining the two laterally directed spikes. These spikes would have allowed rotation yet kept the frontals fixed relative to the postorbital and close to the parietal. In *Varanus* the lateral part of the frontal and parietal fits into a concavity of the postorbital (Frazetta 1962, fig. 1a). The presence of a process anterior and posterior to the fronto-parietal suture also ensures that the frontal and parietal remain close together even though a hinging action is possible.

If the skull of *Hypsilophodon* was mesokinetic then there would have been some other cranial movements (Text-fig. 59B). The postorbital has a long overlapping and smooth contact surface with the jugal so it is likely that a sliding action was possible at this suture. In the palate the pterygoid contacts the articular surface of the basipterygoid process (Text-fig. 5C) at which movement would obviously be possible. The nature of the sutures in the palatal region shows that there was no other plane of movement there. The palatine is firmly sutured to the maxilla as is the ectopterygoid. The ectopterygoid bears a triangular flange of which the apex is medially directed. This flange is recessed into the dorsal surface of the pterygoid (Text-fig. 5C) which borders it anteriorly and posteriorly. Consequently movement of the pterygoid on the ectopterygoid was impossible, which meant that a sliding articulation with the palatine was out of the question.

The relationship between the parietal and bones of the occipital series remains to be considered. Posteriorly the parietal is overlapped by the squamosal, the posterior process of which overlaps the distal part of the paroccipital process (Text-figs. 7B, 8). The occiput in posterior view (Text-fig. 8) appears rather solid but the medial part of the parietal is not sutured to the underlying supraoccipital (Text-fig. 5A). The postero-ventral edge of the parietal and squamosal together form a convex curve (Text-fig. 5B) so the transversely orientated metakinetic axis would have been restricted to a small part of this edge. A hinging action would have involved only a slight movement of the squamosal away from the paroccipital process and this may have been possible (Text-fig. 59B).

No sliding could occur at the joint between the supraoccipital/prootic and the laterosphenoid because of the curved shape of the laterosphenoid and the nature of its suture with the prootic (Text-figs. 4B, 5C, 7B, 9). If the skull was metakinetic then the maximum movement would have been at the anterior end of the laterosphenoid. This is expanded laterally to form a well-developed head (Text-figs. 4B, 6B, 7B) which fits into a depression in the postorbital and frontal, opening ventrally with vertical sides. The depression becomes progressively deeper passing laterally (Text-fig. 7B) so that contact would have been maintained if the head of the laterosphenoid had moved ventrally. The head tapers laterally (Text-figs. 6B, 7B) and the dorsal part of the lateral half is rounded antero-posteriorly (Text-figs. 4B, 7B). The surface of the rounded part of the head and of the lateral part resembles that of the basipterygoid and was possibly an articular surface. In lizards (Frazetta 1962), and presumably in some individuals of *Sphenodon* (Ostrom 1962), the ventral part of the braincase moves slightly antero-posteriorly relative to the parietal. In *Hypsilophodon* the posterior wall of the depression in the frontal and postorbital is quite shallow so, with a slight ventral displacement, such an antero-posterior movement might have been possible. As discussed above (Section d ii) there is a surface on the prootic and basisphenoid which was possibly the area of origin of the M. protractor pterygoidei, one of the muscles necessary to effect the kinetic movements.

Cox (1959) noted that the vena capitis dorsalis passes through the post-temporal fenestra in living reptiles. It is significant that the remnant of the post-temporal fossa is totally enclosing by the paroccipital process in *Hypsilophodon*. In hadrosaurs in which the skull was akinetic Langston (1960) showed that the paroccipital process forms the ventral border to the remnant of the post-temporal fossa. In a metakinetic skull with a close but movable contact between the opisthotic and the squamosal, the vena capitis dorsalis, if it passed between those two bones, would have been subjected to pressure changes. The course of this vessel through the paroccipital process suggests that such a movement occurred because, had it not done so, such enclosure would have been unnecessary. From the nature of the material it is impossible to prove one way or the other but I consider that the skull of *Hypsilophodon* may have been mesokinetic and metakinetic (Text-fig. 59B). However, I do not know what function these movements would have served in a herbivore. It would be helpful to know something of the selective advantages conferred by the quite complex kinetic movements which, according to Frazetta (1962), are retained in the herbivorous lizards *Ctenosaura* and *Uromastix*.

f) *Streptostyly*

A streptostylic skull is one in which the quadrate moves relative to the other bones of the skull. This term is not interchangeable with kinetic because the two types of movement involved can occur independently or together. The head of the quadrate of *Hypsilophodon* is triangular in outline with a rounded articular surface (Text-fig. 4A) which fitted quite closely into a socket in the squamosal (Text-fig. 6B). The quadrate may have been loosely connected to the quadrotojugal but the likelihood of movement was minimal because, although the quadratojugal overlapped the quadrate ventrally, dorsally the situation was reversed. The lateral surface of the quadrate forms an angle of about 50 degrees with the pterygoid flange. Movement of the quadrate relative to the pterygoid must have been in the plane of this flange so the dorsal part of the quadratojugal would have restricted movement anteromedially; the ventral part would have restricted it postero-laterally. The quadratojugal is overlapped by the jugal and, although a slight amount of sliding is conceivable, the parting of this contact necessary for the independent movement of the quadrate is considered unlikely. In addition the presence of the jugal on the lateral surface would have limited the amount of posterior movement.

In medial view the quadrates of R2477 (Text-fig. 4B, Pl. 1, fig. 3) and R192 clearly show the postero-lateral limits of the contact area with the alar process of the pterygoid. This is indicated by a distinct step in the level of the surface. The region of the quadrate on which this outline is preserved is curved in cross-section so that it is concave in medial view. This curved part is on the shaft, the posterior edge of which is sharp and makes an angle of about 110 degrees with the plane of the pterygoid flange. The postero-lateral part of the alar process of the pterygoid would have been curved in cross-section with a convex lateral surface. It is apparent that any movement between the quadrate and the pterygoid must have been one of sliding. The curved distal part of the alar process would have fitted against the concave part of the quadrate shaft and would have limited the anterior movement of the quadrate. In addition the curved nature of this distal part would have reduced the likelihood of any movement of the quadrate away from the pterygoid.

I consider that the contacts with surrounding bones would have prevented any independent movement of the quadrate. However, a slight movement of the quadrate with the quadratojugal and jugal relative to the postorbital, squamosal and braincase may have occurred if, as was possibly the case, the skull was mesokinetic (Text-fig. 59B).

g) *The antorbital fenestra*

In thecodontians such as *Euparkeria* (Ewer 1965) and *Stagonolepis* (Walker 1961) the large antorbital fenestra is bounded dorsally by the lachrymal and ventrally by the maxilla. In *Hypsilophodon* the antorbital fenestra is actually represented by the two internal antorbital fenestrae in the medial wall of the maxilla, visible in lateral view (Text-figs. 4A, B). The lateral opening will be called the external antorbital fenestra while the space totally enclosed by the maxilla is the antorbital fossa (Text-figs. 60C, D). The medial sheet of the maxilla and lachrymal is present in *Heterodontosaurus* and *Fabrosaurus* (Crompton, personal communication), both of which are from the Upper Triassic, but the external antorbital fenestra is large (for *Heterodontosaurus* see Crompton & Charig 1962). In *Parksosaurus* (see Parks 1926, Galton in press) the lateral sheet of the maxilla is large and the external antorbital fenestra is small. In *Dysalotosaurus* (see Janensch 1955) both the external antorbital fenestra and the lateral sheet of the maxilla are small but a large sheet from the premaxilla encloses part of the antorbital fossa. *Camptosaurus* in lateral view is similar and Gilmore (1909 : 214–215) mentioned that the lateral foramina in the maxilla 'are received by a large, elongate cavity situated at the base of the dorsal process between the thin inner and outer walls, and which opens posteriorly'.

The important point is that in these lower ornithopods there is a large fossa which opens posteriorly into the ventral part of the orbit below the eye. This cavity represents the antorbital fenestra, which in thecodontians also opens posteriorly

(Walker 1961, Ewer 1965). Consequently the obliteration of the antorbital fenestra, at least in these lower Ornithischia, was more apparent than real because it was merely enclosed medially and laterally to a varying extent by thin sheets of bone.

The function of the antorbital fenestra of thecodontians has been discussed by Walker (1961) and Ewer (1965). Both agree that in the more advanced forms the fenestra was for the origin of an anterior portion of the pterygoideus muscle. Walker (1961) kept the insertion of this portion on the lower jaw close to the articulation so that it effected a rapid movement of the jaw at the beginning of the bite. Ewer (1965) placed the insertion more anteriorly on the jaw so that this portion provided power for the initial phase of the bite.

In *Hypsilophodon* the only possible exit for a muscle from the antorbital fossa is posteriorly across the floor of the orbit. This opening in R2477 is about 4 mm wide and it is restricted dorso-laterally by the projecting edge of the jugal (Text-figs. 5B, C). As noted above, the M. pterygoideus dorsalis probably originated from the dorsal surface of the ectopterygoid. An anterior portion of this muscle may have extended anteriorly into the antorbital fossa. This portion would have passed across the floor of the orbit, over the edge of the ectopterygoid (Text-fig. 5C) and medial to the coronoid to insert on the lower jaw. Only a small slip or a tendon could have followed this route and the main part of the muscle must have been in the antorbital fossa. However, the morphology of the dorsal surface of the ectopterygoid indicates that, if the M. pterygoideus dorsalis extended anywhere, it would have passed on to the adjacent surface of the palatine. On the anterior part of the palatine there is a slight transverse step which may indicate the limit of such an extension (Text-figs. 5C, 60D).

When discussing the function of the antorbital fenestra it is assumed that the muscle concerned is derived from the M. pterygoideus dorsalis, as is the pterygoideus D of crocodiles (Lakjer 1926), but this anterior extension could have been part of the M. pterygoideus ventralis. In *Hypsilophodon* this latter probably originated from the ventral surface of the pterygoid and ectopterygoid (Text-figs. 4B, 60D). It is possible that a portion of this muscle passed through the vacuity between the ectopterygoid, palatine and maxilla (Text-figs. 5A, 6A) from an origin in the antorbital fossa (Text-fig. 60D). In specimen R2477 this vacuity is a rather square oval, 6 mm × 4 mm. The lateral wall of the maxilla becomes progressively shallower posteriorly and its edge more rounded. The topography of this part of the maxilla suggests that whatever originated from the antorbital fossa may have passed postero-ventrally through this palatal vacuity (Text-figs. 5A, C, Pl. 1, fig. 1, Pl. 2, fig. 2). If a cord be passed from the top of the antorbital fossa to its posterior opening, across the maxilla and through this vacuity, it forms a gentle curve. From the figures of the skull it would appear that a similar course would have been possible in the thecondontians *Euparkeria* (Ewer 1965), *Stagonolepis* (Walker 1961) and *Ornithosuchus* (Walker 1961).

The function of this postulated anterior portion of the pterygoideus in *Hypsilophodon* is not certain. If the insertion of this portion was close to the articulation it would have aided the rest of the pterygoideus in rapidly closing the jaw to effect a cropping action of the anterior horny beaks (function the same if portion was from the pars dorsalis). Such a course would give a very long muscle with a moderately straight course. However, the much more powerful M. adductor posterior, the moment arm of which is quite short, would have been much more effective. If the insertion was more anterior the pull of this muscle would tend to be in the plane of the occlusal surface of the teeth. As a result this would add to the shearing force at these surfaces (see Section h). To be effective this insertion should have been some way forward in the region below the coronoid but there is no evidence to show whether or not this was the case.

The enclosure of the antorbital fenestra in lower ornithischians without its obliteration is rather interesting. These forms could be regarded as demonstrating stages in its closure, the space enclosed having no function, but this is not very satisfactory. In the line leading to *Parksosaurus* this fossa was retained from the Upper Triassic right through to the Upper Cretaceous (Edmonton Formation) and it still retained a posterior exit. If this fossa was functionless it is surprising that it remained for such a long time in a region which was important in supporting the tooth row. A slip of the pterygoideus muscle (pars ventralis and/or dorsalis) probably originated from this space and this slip must have remained functional in these lower ornithopods.

h) *Jaw action*

Information concerning the mode of action of the jaws can be deduced from the arrangement and wear of the teeth, the nature of the jaw articulation and the lines of action of the musculature as reconstructed from the form of the skull. In *Hypsilophodon* there are several features indicating that an antero-posterior movement of the lower jaw was not possible. The inclination of the glenoid surface of the articular at about 30 degrees to the tooth row (Text-fig. 10A) would have prevented any significant retraction of the mandibles. The anterior convergence of the tooth rows (Text-figs. 6A, 10B) would have prevented any mandibular protraction. In addition the tooth rows are slightly curved with the individual teeth forming a rather jagged edge. It is therefore concluded that mandibular movement consisted only of a hinge movement about the condyle of the quadrate. The occlusal surfaces in *Hypsilophodon* are at an angle of about 10 degrees to the vertical for anterior teeth or about 25 degrees for more posterior teeth. These angles are rather approximate because the precise orientation of the maxillae is not absolutely certain. The occlusal surfaces were certainly not vertical because in that case the lower jaw would not fit between the maxillae.

In *Hypsilophodon* the maxillary and dentary teeth are thickly enamelled on one side and are transversely curved in opposite directions (Text-fig. 61). The convex surface bears thick enamel in both cases and, as the enamel was more resistant it formed a sharp edge while the rest of the tooth formed an obliquely inclined occlusal surface (Text-figs. 15, 60, 61). The sharpness of the enamelled edge is enhanced by the presence of serrations formed by the wear of the longitudinal ridges on the enamelled surface of the crown. In particular the apex ridge of each dentary tooth is very large and formed a prominent spike on the cutting edge (Text-figs. 15c, 16c).

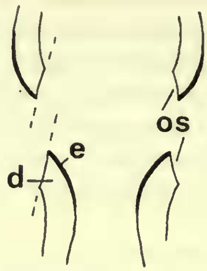

FIG. 61. *Hypsilophodon foxii.* Diagrammatic cross-section through dentition assuming that occlusal surface of maxillary and dentary teeth equally spaced apart. Abbreviations : de, dentine ; e, thickly enamelled surface ; os, occlusal surface.

When a force is applied across two obliquely inclined but parallel surfaces it can be resolved into two components using a parallelogram of forces. One component, that responsible for a crushing action, acts perpendicular to the occlusal surfaces. The other component, that responsible for a shearing action, acts parallel to the occlusal surface. With the angle of the occlusal surfaces at about 10–25 degrees to the vertical it is apparent that the shear component represented the greater proportion of the total force exerted across the obliquely inclined occlusal surfaces of *Hypsilophodon.* In addition, the sharp enamelled edges of both teeth would have had a cutting action.

The lateral relationship of the occlusal surfaces of the maxillary and dentary teeth cannot be determined from the skull material. The above analysis is based on the assumption that the lower teeth were the same distance apart transversely as the corresponding uppers (Text-fig. 61). However, the dentary teeth were probably closer together so that an oblique movement was possible with the teeth of only one side in opposition at a time. The amount of shift needed is quite small and, because the articulation surface of the quadrate (Text-fig. 6A) is much wider than that of the articular (Text-fig. 10B), such a movement may have been possible. This oblique movement would have resulted from the asymmetrical contraction of the jaw adductor muscles. With such a movement the sharp enamelled edges would have cut past each other and the action at the occlusal surface would have been almost exclusively one of shear.

The jaw adductor muscles insert on to the coronoid and the adjacent bones (Text-figs. 59, 60D) and their force is applied between the fulcrum (the glenoid cavity) and the resistance (food between the teeth). As a result, the lower jaw forms a third class lever with the adductor muscles acting somewhat obliquely. When an obliquely inclined muscle inserts on to a straight lever the effective force (i.e. the moment arm) can be increased by elevating the point of application above the axis or, alternatively, the fulcrum can be depressed below the line of the tooth row. In both cases the force exerted by the muscle is increased without decreasing the gape possible ; this would be decreased if the point of insertion were moved along the axis further away from the fulcrum. In *Hypsilophodon* the coronoid process is large so that the moment arms of the M. pseudotemporalis and the M. adductors externus, medius and profundus were lengthened (Text-fig. 59A). The glenoid cavity is set below the level of the tooth row so that the moment arm of all the main adductor muscles was increased.

The average line of action, together with the moment arm, is indicated for each muscle in the reconstruction of the skull (Text-fig. 59A). Although not absolutely accurate this reconstruction is adequate for general conclusions regarding the relative size of each muscle and its moment arm. The M. pseudotemporalis and the three divisions of the M. adductor externus were the main adductors. The M. pseudotemporalis has the longest moment arm but it was probably not so important as the other three muscles combined (they have a common line of action). The M. adductor mandibulae posterior was a large muscle but it had a small moment arm. Consequently it was important for the initial closing movements but then probably functioned mainly to prevent disarticulation of the jaw. The M. pterygoideus dorsalis and ventralis were probably not very large. Their extremely small moment arm means that they probably functioned chiefly to aid the M. adductor posterior in preventing disarticulation of the lower jaw. As discussed in Section (g) it is possible that an anterior portion from the antorbital fenestra inserted more anteriorly on the jaw (Text-fig. 60D). The only muscle acting to open the jaw, the M. depressor mandibulae, had a small moment arm. This means that the muscle had a fast action but exerted little force. However, there was little resistance to overcome and the weight of the lower jaw itself would have aided its own depression. It is apparent that the main adductors had a good mechanical position and the slight forward inclination of the quadrate helped it to resist the forces developed. The teeth formed an efficient apparatus for dealing with plant food as they combined cutting, shearing and crushing.

The food was obtained initially by the cropping action of the anterior horny beaks. As Nopcsa (1905) noted, the premaxillae are rugose anteriorly, indicating the presence of a horny beak. The pointed predentary has a fairly smooth outer surface but the only specimen available (Text-fig. 11) is from a small individual. The predentary was probably also covered by a horny beak because this is the case in other ornithischians (e.g. hadrosaurs, Ostrom 1961). More posteriorly the premaxillary teeth presumably bit outside the predentary. In ventral view (Text-fig. 6A) there is a step between the line of the tooth row of the premaxilla and maxilla. In addition, much of the maxilla is visible lateral to the tooth row which, as a result, is overhung (Text-fig. 3). The dorsal view of the lower jaw (Text-fig. 10B) shows a similar situation with much of the dentary lying lateral to the tooth row. I believe that the corner of the mouth probably did not extend much further back than the anterior end of the maxillary tooth row. Consequently the mouth was small and there was quite a large space lateral to the tooth rows of the maxillary and dentary which was necessary if the animal was to chew its food (see below: 150) The tongue would have moved the food around so that it was chewed several times while the space lateral to the tooth rows would have received the food prior to its next passage between the occlusal surfaces.

VII. ASPECTS OF POST-CRANIAL ANATOMY

a) *Individual variation*

There is a surprising amount of variation between the few specimens of *Hypsilophodon foxii* represented by articulated material. Certain of these variations are found also in *Thescelosaurus neglectus* (see Galton in press *a*). Details of variations with age and sex are available for *Protoceratops andrewsi* (Brown & Schlaikjer 1940) but, apart from this, there is very little information in the literature concerning variation in other species of dinosaur.

The most notable variation is the presence of the additional sacral rib in the hexapleural sacrum in contrast to the pentapleural type (see page 57). In Ornithischia the number of sacral vertebrae may vary between different species of the same genus, e.g. *Camptosaurus dispar* with 5 and *C. browni* and *C. depressus* with 6 (Gilmore 1909) ; *Iguanodon mantelli* with 5 and *I. bernissartensis* with 6 (Boulenger 1881, Dollo 1883). These are generally considered to be valid species. However, in the case of *Iguanodon,* van Beneden (1881) regarded the variation in the sacral count as an individual or sexual variation ; Hooley (1912) also regarded it as a sexual variation (with *I. mantelli* as the female), although later (1925) he treated the two forms as separate species. Nopcsa (1918, 1929) considered that male ornithischians were characterized by the presence of extra sacral vertebra(e). In *Camptosaurus* the sacral difference is associated with several other differences (see Gilmore 1909, Nopcsa 1918, 1929) while in *Iguanodon* there are even more (see Nopcsa 1918, 1929, Dollo 1883, Abel 1927). However, in *Hypsilophodon* there are only a few other significant differences associated with that of the sacrum. In the pentapleural specimen R196, when compared with the hexapleural specimens, the peduncle of the ilium is narrower, the facets on the ilium for sacral ribs 2 to 5 are more anteriorly placed and the sub-acetabular part of the ischium is longer. A size difference is often used as a basis for specific separation with fossil material but there is no justification for this because the largest sacra of each type are about the same size (length of first three centra 75 mm in R193, 71 mm in R8422). The close similarity of the teeth and post-cranial skeletons of individuals with the two sacral types clearly shows that they are the same genus *Hypsilophodon.* The specific identity or separateness of the two sacral types depends on the taxonomic significance attached to the presence of the additional sacral rib.

In living birds the number of sacral vertebrae does not vary within a species (Nopcsa 1929) and this is apparently also the case in reptiles (Werner 1895). However, the sacral count can vary in man : there are usually five lumbar and five sacral vertebrae but this count can be four and six or six and four (Brash & Jamieson 1943). Consequently the number of sacral vertebrae (and hence ribs) can vary within a species. In view of the position in man and the individual variation shown by R5829 I consider that the two sacral types are best regarded as individual variations of *Hypsilophodon foxii.* However, even if the two types were to be regarded as separate species it would be inadvisable to give them taxonomic status because the sacral type of the holotype of *Hypsilophodon foxii* is not known.

The presence of an extra sacral rib (or vertebra) cannot be regarded as an age variation because the smallest specimen available (R5830) already has the extra sacral rib. The sacral difference in *Hypsilophodon* probably represents a sexual dimorphism, with the hexapleural type as the male. The sacral type can be determined in only eight individuals, there are five hexapleural forms and three pentapleural forms. It is interesting that Nopcsa (1929) used the high ratio of *Iguanodon bernissartensis* (regarded as the female) to *I. mantelli* (23 : 1) at Bernissart as evidence for herding in this species (*I. mantelli*).

The specimens of *Hypsilophodon* show quite a few other variations which were mentioned in the descriptions of the individual elements. The differences that appear to be correlated with the sacral difference have already been noted. Individual variations relate to the presence of the cavity in the premaxillae ; the contacts of the lateral sheet of the maxilla with the premaxilla and with the lachrymal and jugal ; various features of the sacrum ; the degree of ventral curvature of the anterior process of the ilium and the size of the medial ledge along its ventral edge ; the opening or closure of pubic foramen in small or large individuals ; the cross-section of the post-pubic rod ; the outline of the ventral junction between the head and shaft of the ischium ; the degree of development of the depression at the base of the fourth trochanter of the femur ; the form of the edges of the tibia ; and the outline of the posterior junction between the shaft and the blade of the scapula. Variations related to increased size probably include the ankylosis of the neural arches, ribs and centra of the sacral vertebrae ; the presence of strong sutural ridges between the scapula and coracoid ; the greater angularity of the edges of the scapula and coracoid and the greater degree of twisting of the shaft of the scapula and humerus.

b) *The first sacral rib*

In the reconstructions of *Hypsilophodon* by Hulke (1882), Marsh (1895, 1896*a*, *b*), Swinton (1934, 1936*a*) and von Huene (1956) the iliac peduncle is shown square-ended with the first sacral rib fitting on to the base of the anterior process. However, the first sacral rib actually fits against the iliac peduncle (Text-figs. 47A, 50B, 51B). This is the same as in *Thescelosaurus* (see Gilmore 1915, Galton in press *a*), *Camptosaurus* (see Gilmore 1909) and *Dysalotosaurus* (see Janensch 1955).

The peduncle region in *Hypsilophodon*, like that in most other Ornithischia, is quite slender and roughly triangular in cross-section (Text-fig. 47B) with the facet for the first sacral rib facing dorso-medially. As a result of the wedge-shaped cross-section the acetabular margin of the peduncle is horizontal yet there is a broad sutural surface with the first sacral rib. The slender peduncle region is therefore backed by the first sacral rib through which the thrust from the femur is transmitted to the vertebral column. This becomes progressively more important as the vertebral column is held more vertically. The first sacral rib is extremely thick and almost cubical (Text-fig. 27). The ends of sacral centra 1 and 2 form a large contact surface and then flare out to embrace the proximal part of the first sacral rib (Text-fig. 27B). This is also the case in *Thescelosaurus*, *Camptosaurus*, the English '*Camptosaurus*' *prestwichi* (see Gilmore 1909) and *Dysalotosaurus*. In these dinosaurs, as was probably the case in all lower Ornithopoda, the first sacral rib performed a key rôle in strengthening the iliac peduncle.

In *Hypsilophodon* the additional sacral rib in the hexapleural type of sacrum must have acted as an anterior brace for the first sacral rib and, in addition, helped to spread the thrust anteriorly. In R5829 this action was enhanced by the sutural union of the new sacral rib with the transverse process of the first sacral vertebra. It is perhaps relevant that the peduncle is more expanded transversely in forms with a hexapleural sacrum than in the other type but more specimens are needed to confirm this difference and, in addition, to provide more information about the union between the neural spines. In R195, which has a hexapleural sacrum, the edges of the neural spines of sacral vertebrae 1 and 2 are thick and closely united by a suture (Text-figs. 25E, F, 27B). Such a suture would further strengthen the union between the two vertebrae supporting the first sacral rib. However, the union between the neural spines is variable even in the few sacra available.

The iliac peduncle is slender and only the tip could have contacted the pubis. Here there is a small rugose area running diagonally across the end of the peduncle (Text-figs. 47B, 51C). This sutural surface is surprisingly small in comparison with the corresponding surface on the pubis (Text-fig. 52A). Anterior to the concave acetabular region, which in life was probably covered by cartilage, there are two distinct areas which are separated by a slight edge (Text-figs. 46A, 52A). Anteromedially there is a slightly convex area (sa. r. 1) of which the plane is inclined slightly more medially than that of the similar but smaller outer area (il.). It would appear that the ilium sutured with the outer area while the inner one was for the first sacral rib. The ventral surface of this rib in R195 (well preserved on left side, Text-fig. 27C) forms a large flat surface against which the pubis fitted. Consequently the pubis contacted the first sacral rib in addition to the ilium. A similar contact between the pubis and the first sacral rib is present in *Thescelosaurus* (see Galton, in press *a*) but, because the relevant areas of the ilium, pubis and sacrum are not known, it is impossible to determine the position in *Parksosaurus*. It is probable that the pubis articulated with the first sacral rib in *Dysalotosaurus*, to judge from the figures by Janensch (1955), but this possibility is not mentioned. The acetabular aspect of the pubis is very similar to that of *Hypsilophodon* but the broad anterior articular surfaces form one rounded curve. The peduncle of the ilium is almost identical in internal and external views but the acetabular view is not given. The first sacral rib has the same square shape but only the lateral view is given. The pubis of the mounted skeleton of *Iguanodon atherfieldensis* in the British Museum (R5764) has a broad dorsal surface which contacts a corresponding surface on the first sacral rib when the ilium is in articulation with both bones ; Hooley (1925) does not mention this.

c) *Limb articulation and posture*

i) FORELIMB

Both scapulae were displaced in specimen R196 so the original position cannot be determined. However, in several specimens of *Iguanodon* and hadrosaurs the scapula is preserved lying parallel to the vertebral column which, as Lull & Wright (1942) noted, was probably its position in life. It is reasonable to assume that this was also the case in *Hypsilophodon* (Text-fig. 62). The ventral edge of the coracoid is rough and bore a cartilaginous extension so there is no direct evidence concerning the angle at which the coracoid was held. When the transverse curve of the scapula and coracoid (Text-fig. 34B) is compared with that of the anterior dorsal ribs it appears that the coracoid probably made an angle of about 35 degrees (± 5 degrees) above the horizontal.

In reconstructions of bipedal dinosaurs the humerus is usually shown held vertically below the glenoid. Gregory (*in* Osborn 1917) and Sternberg (1940, 1965) pointed out that in this position the head of the humerus is out of the glenoid cavity. They concluded that the humerus was held more laterally while Sternberg (1965) thought that the ornithopod humerus was actually held horizontal. If maintaining contact between the limits of the articular surfaces of the humerus and the glenoid cavity was the factor limiting the range of movement, then this range was very restricted in the transverse plane. In *Hypsilophodon* this range would have been about 30 degrees: from 35 to 65 degrees to the vertical (or 90 to 120 degrees to the lateral surface of the coracoid). However, in the crocodile the range of movement is at least 90 degrees: from horizontal and lateral to vertically below the body in the high walk and the gallop (Cott 1961). It would be surprising if the range of movement was less than this in *Hypsilophodon*. It should be noted that the articular surface of the humerus is formed by all of the proximal end, not just the convex surface of the dorso-laterally directed 'head' (see Text-fig. 38). Consequently this 'head' can be completely out of the glenoid (i.e. visible in lateral view) but the more medial part of the articular surface is still in the glenoid. Although the humerus could have been held much more laterally than shown in most reconstructions the vertical pose was probably quite normal. The anterior limit of movement of the humerus can be determined because the anterior edge of the head comes up against the scapula. The edge of the glenoid in this region is reduced, forming a depression (Text-fig. 35A) into which fitted the humerus. The anterior limit is such that the delto-pectoral crest is approximately perpendicular to the adjacent lateral surface of the scapula.

The elbow joint, radius and ulna are similar to those of other dinosaurs. The articulations at the wrist cannot be determined because this region is badly preserved. The manus was undoubtedly capable of grasping. The phalanges of the first three digits are well formed (Text-fig. 41) and the third digit, with four phalanges, must have been capable of a large amount of flexion. Distally the fifth metacarpal has a definite condylar end with a well-defined articular surface which undoubtedly carried at least one phalanx. This metacarpal is certainly small but this does not necessarily mean that digit V was reduced. Metacarpal V of *Iguanodon*, relative to the other metacarpals, is proportionally only slightly larger than that of *Hypsilophodon* yet it bears four well-developed phalanges – the longest set in the hand (see Hooley 1925). In hadrosaurs the fifth metacarpal is about a third of the length of metacarpal III but it still bears three small phalanges (see Parks 1920 for *Kritosaurus*, Lull & Wright 1942 for *Anatosaurus*).

Proximally the lateral corner of metacarpal IV (Text-fig. 41B) closely resembles the medial corner of metacarpal I and, in the absence of metacarpal V, it would be assumed that digit V was completely reduced. This indicates that metacarpal V was not held alongside metacarpal IV but set at an angle, though this has probably been somewhat exaggerated as preserved in this specimen. The proximal end of metacarpal V, which articulated with the ulna, is slightly concave with a relatively extensive articular surface dorsally and ventrally. This indicates that quite a wide range of movements were possible, including a certain degree of ventral rotation. With metacarpal V in the same plane as the other metacarpals (Text-fig. 41) its phalanges would face ventro-medially because, as a result of the twisted shaft, the distal articular surface is set at an angle of about 135 degrees to the horizontal (a line through the transverse plane of the carpus). In this feature it is comparable to the human first metacarpal, the distal end of which makes a similar angle (45 degrees in this case). The condylar regions of metacarpals II to V are horizontal in man. However, as preserved it appears that in *Hypsilophodon* those of metacarpals II and III are set at an angle of 45 degrees to the horizontal so that these digits face ventro-laterally (Text-fig. 41B). With the fifth digit facing ventro-medially its joint surfaces are perpendicular to those of the second and third digits. This reduced the amount of ventral rotation necessary before the fifth digit was truly opposable. However, more material is needed to confirm the nature of the distal articular surfaces of metacarpals II, III and V.

ii) HINDLIMB

The femur was certainly held beneath the body. With its head set on a well-developed neck perpendicular to the shaft, no other pose was possible. The distal surface is somewhat obliquely inclined in posterior view (Text-fig. 54D). However, the corresponding surface of the tibia slopes the other way (Text-fig. 56B) so that the tibia moved more or less antero-posteriorly on the femur. The range of movement of the tibia cannot be determined because this depended on the restraining action of the knee capsule ligaments. The head of the fibula articulated with the groove on the lateral surface of the outer condyle of the femur when the knee was fully flexed.

In dinosaurs the joint between the tibia/fibula and the proximal tarsals was rendered immobile in various ways to form a mesotarsal joint. In ornithischians the joint is between the proximal and the distal tarsals, with both the astragalus and the calcaneum firmly attached to the tibia/fibula. In *Hypsilophodon* the distal end of the tibia is broad and backs the calcaneum as well as the fibula. The astragalus wraps round the inner malleolus with an anterior ascending process which was attached by ligaments to the adjacent part of the tibia (strong insertion markings here, see Text-fig. 56G). With a digitigrade pose the metatarsals, because they meet the tibia at an obtuse angle, would tend to rotate the astragalus anteriorly but the anterior process of the astragalus prevented this. The proximal tarsals, although firmly attached to the tibia and fibula, were not fused to them because they have shifted in most specimens. However, apart from small specimens (e.g. R5830) it appears that the astragalus and calcaneum were ankylosed together because no division is visible between them in larger specimens.

The functional ankle joint was between the proximal and distal tarsals, which were firmly attached to the tibia/fibula and to the metatarsus respectively. The range of possible movement at this joint is easily determined because the markedly convex articular surface of the calcaneum must have retained contact with the second distal tarsal. This gives a minimum angle of 60 degrees between the tibia and the metatarsus and a maximum of 180 degrees.

There was probably no movement between the distal tarsals and the metatarsals. Distal tarsal I fits across the joint between metatarsals II and III, engaging a small boss on metatarsal II, and there are well-developed radial striations indicating a strong ligamentous connection. The corresponding surfaces of distal tarsals I and II are of similar form so that they made a good fit. There were probably cartilaginous elements for the rest of metatarsals I and II which, together with the proximal and distal tarsals, were surrounded by a strong joint capsule. Metatarsals I to IV were closely applied to each other with broad contact surfaces so it is very unlikely that there was any movement between them and the metatarsus was therefore rigid.

In the reconstructions of the foot by Hulke (1882, pl. 82) and Abel (1912, fig. 293) the fifth metatarsal, relative to the other metatarsals, is shown much too long; but in Marsh (1895, fig. 9), Heilmann (1926, fig. 115) and Romer (1966, fig. 241) it is correctly drawn. In all these reconstructions the fifth metatarsal is shown lateral to metatarsal IV and also, except in those by Hulke and Romer, closely applied to the lateral edge of metatarsal IV. Proximally this edge is moderately rounded (Text-fig. 57H) but it soon becomes extremely sharp-edged so it is unlikely that metatarsal V occupied this position. The second distal tarsal is wedge-shaped in lateral view (Text-fig. 57M) with a broad and rounded ventral articular surface (Text-fig. 57J) for metatarsal V. In S.M. 4129 metatarsal V is preserved across the ventral surfaces of metatarsals IV and III with its proximal end in contact with distal tarsal 2. Metatarsal V is on the ventral surface of the metatarsus in all the other specimens where it is preserved (R193, R196, R200) and this was probably its natural position. In *Thescelosaurus* metatarsal V is ventral to metatarsal IV (Gilmore 1915, fig. 16) while Parks (1926 : 37) noted that in *Parksosaurus* metatarsal V is 'known only by a small bone under the palmar surface of the left foot'.

iii) QUADRUPEDAL OR BIPEDAL POSE AND THE POSTURE OF THE VERTEBRAL COLUMN

In the reconstructions by Hulke (1882) and Heilmann (1916) *Hypsilophodon* is shown in a quadrupedal pose while Marsh (1895), Abel (1922, 1925), von Huene (1956), Swinton (1962) and Colbert (1965) show it as a biped. In the reconstructions by Smit (*in* Hutchinson 1894) and Swinton (1934, 1936*a*, 1954) both poses are given. Heilmann (1916, 1926) noted that *Hypsilophodon* was not normally bipedal because the structure of its pelvic girdle was similar to that of the completely quadrupedal *Stegosaurus*. Consequently the form and proportions of the limbs must be considered to see whether or not *Hypsilophodon* could have run quadrupedally.

The manus is very small, when compared with the pes from the same individual (Text-figs. 41, 58), and it is adapted for grasping rather than for locomotion. The long bones of the forelimb are smaller and much more slender than those of the hindlimb. Consequently it is unlikely that the forelimb supported the body while the animal was running. *Hypsilophodon* has a forelimb 58·6 per cent of the length of the hindlimb ; if the metacarpals and metatarsals are included, the ratio is 52·5 per cent. The hindlimb would have greatly outstepped the forelimb and this would have been especially significant if the animal remained on all fours while trying to run. In order for the hindlimbs to make their full stride while the animal is quadrupedal the acetabulum must have been much higher than the glenoid cavity. As a result the dorsal vertebral series would have to be obliquely inclined and rise upwards to the pelvis. The presence in R196 of an uninterrupted series of ossified tendons from the fifth dorsal vertebra to the end of the sacrum indicates that this part of the column was relatively rigid with only a limited amount of bending in the sagittal plane. The sacral series would also be obliquely inclined and the column would curve downwards again only at the anterior part of the tail. These points are shown in Heilmann's reconstructions (1916, fig. 76) and the dorsal and sacral series are at an angle of 25 degrees to a line passing through the manus and pes. The knee is still quite strongly flexed and for a full stride this angle would be even larger. The overstepping effect and the resulting pose make it impossible for *Hypsilophodon* to have run quadrupedally.

To run efficiently it is important that the limb be positioned under the body because this lengthens the stride, improves the leverage exerted by each segment of the limb during propulsion and reduces the amount of lateral swinging of the limb during recovery. The lengthening of the distal parts of the hindlimb is an adaptation for fast running with a fore and aft movement of the limb but the distal parts of the forelimb are not elongated (Table V). In fast running quadrupedal ungulates and carnivores the fore and hindlimbs are modified to a comparable degree (see ratios in Gregory 1912). The restriction of cursorial adaptations to the hindlimbs in *Hypsilophodon* clearly shows that the animal was bipedal.

To move bipedally, the hindlimb should be long relative to the trunk (Ewer 1965). The trunk length can be taken as the distance between the glenoid cavity and the acetabulum. If the leg length be taken as femur and tibia, then the ratio leg length : trunk length is 1·26 which is higher than in modern lizards which are facultatively bipedal (see Ewer 1965, fig. 16 – *Basiliscus* – 1·05). However, because *Hypsilophodon* was digitigrade, the third metatarsal should also be included in the leg length, increasing the ratio to 1·59. The trunk is clearly short enough, relative to the hindlimb, for bipedal locomotion. The tail, which is an important balancing organ for facultatively bipedal lizards (Snyder 1962), is sufficiently long in *Hypsilophodon* for this purpose. In addition the rigidity of the posterior two-thirds of the tail, which is ensheathed in ossified tendons, would increase its efficiency as a balancing organ. The small size of the head and forelimbs made balancing easier because it reduced the weight anteriorly. It is therefore apparent that *Hypsilophodon* ran bipedally and could not have done so quadrupedally.

As discussed elsewhere in detail (Galton 1970) I consider that the sacrum of hadrosaurs and iguanodontids was held horizontally while running. This is the pose in living bipeds apart from primates and facultatively bipedal lizards. It was

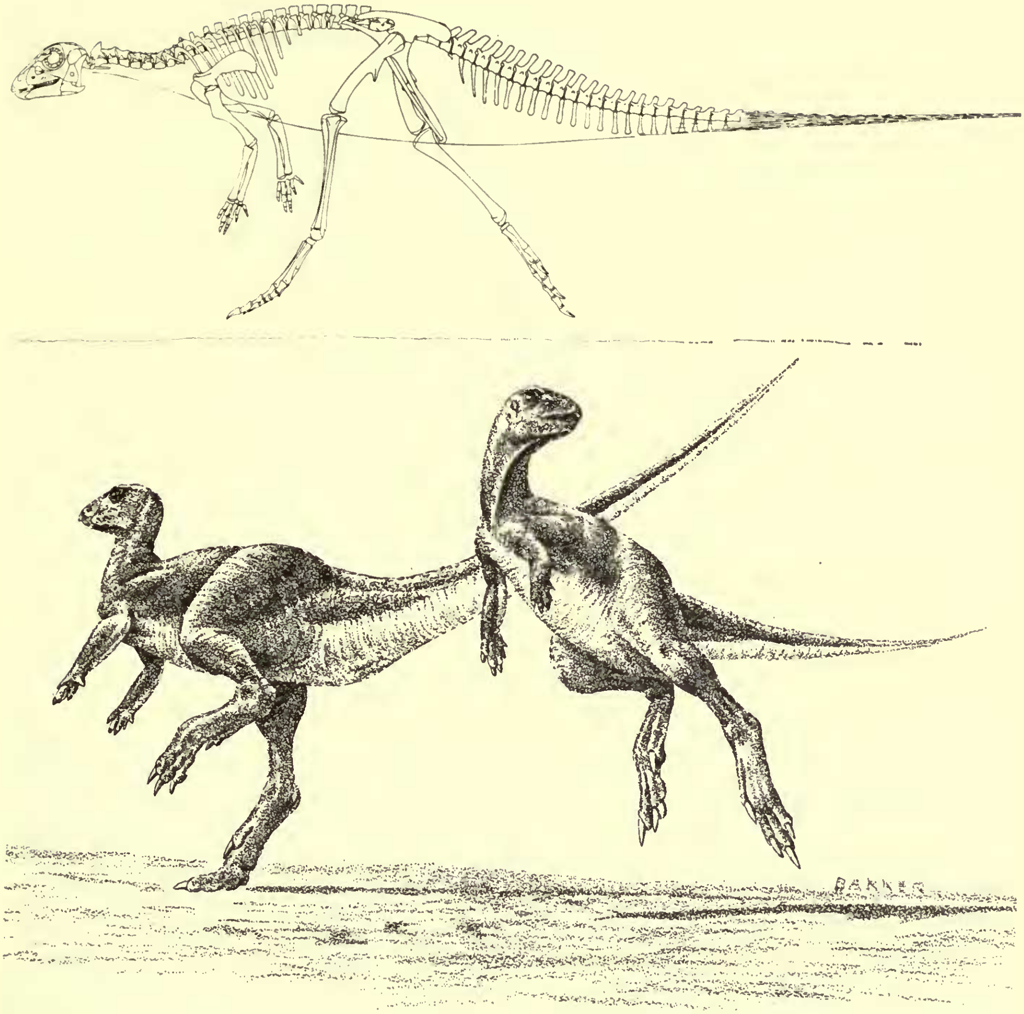

Fig. 62. *Hypsilophodon foxii*. Skeletal and flesh reconstruction showing bodily proportions of an animal about 1·36 m., or 4.5 ft. long (based mainly on R 196, see p. 19). Flesh reconstruction kindly provided by Mr R. T. Bakker of Harvard University.

probably the case in *Hypsilophodon* but the anatomical evidence is not nearly so conclusive as it is for hadrosaurs. Ossified tendons are well developed in *Hypsilophodon* but there is no rhomboidal pattern comparable to that in hadrosaurs. However, this would not seem necessary because *Hypsilophodon* is quite small (specimens known up to 2·28 m). Indeed, the presence of any ossified tendons in an animal of this size is surprising. The tendons of the dorsal series, arranged in parallel rows, would have been quite adequate to prevent a ventral sagging of the column in a horizontal pose and this was probably their function.

The pubic peduncle of the ilium (Text-figs. 46A, 48, 49) is slender but this region was not weak because it is backed by the massive first sacral rib (see Section b), through which the thrust of the femur would have been transmitted to the vertebral column. The vertebral column could have been swung to 40 degrees above the horizontal, the standard 'upright pose', without any danger. However, with a horizontal vertebral column the femur would still bear against the strongest part of the ilium. The central part of the acetabular margin is the thickest and it has the maximum height of ilium above it. In addition the thrust from the femur would be distributed much more evenly through the sacral ribs and would be perpendicular to the vertebral column.

Hypsilophodon was undoubtedly bipedal except when resting on the ground. In slow walking the vertebral column was probably held at about 30 degrees to the horizontal. In this 'upright' pose the animal was in the most advantageous position for catching sight of predators and it could reach foliage at a higher level than if it was quadrupedal or horizontal. However, when running it would seem likely that the vertebral column was held more or less horizontally (Text-fig. 62). This pose, which is the most effective for fast running, is only possible if the animal is completely adapted for bipedal locomotion and has a tail that can provide the necessary counterbalance.

VIII. WAS *HYPSILOPHODON* ARBOREAL?

a) *Historical survey*

Since Hulke (1882 : 1055) concluded that '*Hypsilophodon* was adapted to climbing upon rocks and trees' there has been a considerable amount of discussion on this matter. Abel (1912) argued from the structure of the hind-foot that *Hypsilophodon* was arboreal and that in this it retained the original habitat of the ancestor of all the dinosaurs. In his reconstruction the first toe is shown as being opposable to the remaining three toes, which are shown curving strongly backwards (Text-fig. 63). Abel said that this curvature was natural, rather than due to a post-mortem contraction of the tendons, because the position and attitudes of the articular surfaces would permit no other reconstruction. He considered that this was not a raptorial foot because the structure of the teeth clearly showed that *Hypsilophodon* was herbivorous. Abel concluded that the opposability of the hallux in combination with the strong flexural capabilities of the remaining toes clearly proved that *Hypsilophodon* was arboreal. He suggested that the foot was used to grip round branches as in an arboreal bird.

Heilmann (1916) agreed that *Hypsilophodon* lived in trees but regarded this as a secondary adaptation from a ground-living ancestor. He believed that, because the first metatarsal of *Hypsilophodon* was shortened exactly as in the ground-living dinosaurs, the ancestor of *Hypsilophodon* must also have been terrestrial. A result of this shortening of the first metatarsal is that the first toe arises at a higher level on the foot than the other three toes. Heilmann thought that this would have prevented *Hypsilophodon* from gripping like an arboreal bird in which all the toes arise

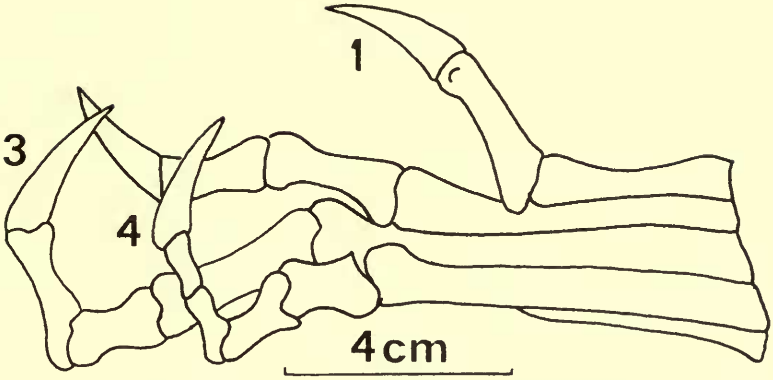

FIG. 63. *Hypsilophodon foxii.* Pes as figured by Abel, based on R196 and figures in Hulke (1873, 1882). After Abel (1912, fig. 283).

at the same level. He felt that the foot was more reminiscent of that of a monkey and, as a result, this secondary adaptation to an arboreal mode of life was analogous to that of the tree kangaroo *Dendrolagus*.

Abel (1925) admitted the correctness of Heilmann's conclusion that *Hypsilophodon* was secondarily arboreal. He opined that the first metatarsal was not further reduced because it was probably used in climbing and extended the analogy with *Dendrolagus* as a basis for reconstructing the pose of *Hypsilophodon*. He thought that the sharp and strongly arched claws of the hind-foot of *Hypsilophodon* would have rendered movement on the ground difficult. He referred to his own reconstruction of the fore-arm (1911) and pointed out that in *Hypsilophodon*, in contrast to the other dinosaurs, the radius was distinctly bowed. He cited Carlsson (1914), who had shown that *Dendrolagus* differed in the same manner from the large ground kangaroo *Macropus*. Carlsson regarded this enlargement of the space between the fore-arms in *Dendrolagus* as an adaptation to an arboreal mode of life.

Heilmann (1926) disagreed with Abel's conclusion that *Hypsilophodon* was arboreal (and, presumably, with his own similar conclusion of 1916). He pointed out that the cursorial *Procompsognathus triassicus* has ungual phalanges which are even more markedly bent than those of *Hypsilophodon*. Although Abel's reconstruction of the foot was based mainly on the figures of Hulke, Heilmann noted that it did not look like these ; furthermore, the individual elements did not agree with the measurements given by Hulke. In addition Heilmann thought that in Abel's reconstruction the first toe would collide with the second metatarsal. He again pointed out that the proximal position of the hallux made it impossible for *Hypsilophodon* to grasp in a fashion similar to that of an arboreal bird. In order to grip a branch the first metatarsal of *Hypsilophodon* must have been movable, as is the first metacarpal in the human hand. Heilmann showed that this was not the case by quoting Hulke (1882 : 1053), who wrote that the proximal ends of the metatarsals 'are in closest mutual apposition'. Heilmann considered that the foot was not specialized for climbing. He reconstructed the foot using Hulke's figures, and the toes are shown straight with no opposability of the hallux. He also thought that the hand was not specialized for climbing. Heilmann reiterated his belief that *Hypsilophodon* was quadrupedal (see above, page 127) but did not explain why this would have prevented *Hypsilophodon* from being arboreal, especially as his reconstruction (1916) showed *Hypsilophodon* climbing with a quadrupedal pose. Lastly, he pointed out that the presence of dermal armour was unexpected if *Hypsilophodon* was a tree climber, because arboreal animals are not usually so equipped.

Abel (1927) noted Heilmann's conclusion that *Hypsilophodon* was not arboreal but did not answer any of the points raised. He admitted that the tail of *Hypsilophodon* could not have been prehensile because of the ossified tendons (an objection that was not raised by Heilmann) but noted that a non-prehensile tail occurs in some tree-geckos. Abel also took further examples from Carlsson (1914) to show that the enlargement of the space between the fore-arms is an arboreal adaptation.

Swinton (1936) suggested that the arm in *Hypsilophodon* had a greater range of brachial movement than in *Thescelosaurus*, *Camptosaurus* or *Iguanodon*. The reasons given were the more medial position of the articular head of the humerus, the more proximal position of the delto-pectoral* crest and the fact that the humerus is longer than the scapula. Swinton admitted that the hand was not specialized for climbing. However, he pointed out that the three relatively elongated middle digits and the long, thin, pointed and curved unguals show that the hand was suitable for grasping, provided that no great weight was to be supported. Concerning the foot he noted that, even in Heilmann's reconstruction (1926), the first metatarsal is shown diverging distally from the rest. He considered that the first digit was opposable even though it was more proximally placed on the metatarsus. He pointed out that in the human hand some opposable action of the thumb is still possible even when the first metacarpal is forcibly kept against the second. However, Swinton (1936) admitted that the amount of opposability was probably exaggerated by Abel who argued on the basis of an unnaturally retracted foot.

Though some elongation of the hindlimb has taken place, the tibia being longer than the femur, Swinton (1936) pointed out that truly cursorial animals have an elongate metatarsus – a modification lacking in *Hypsilophodon*. Swinton also noted (1936 : 576) that in '*Hypsilophodon* (and even more so in *Thescelosaurus*) the fourth trochanter extends at least to the distal half of the bone, and this suggests that though the muscles may have been powerful their mere presence in this position hampered femoral movement to some extent'. From the structure of the hindlimb he concluded that, although bipedal, *Hypsilophodon* could not run fast but that the musculature was sufficient for climbing and balancing. In addition he noted that the tail must have been a rigid structure because of the presence of ossified tendons and that it must have helped in balancing. Swinton (1934) noted that dermal armour was shown in Heilmann's reconstruction (1916) but that, as it was only light, this was not a serious objection to *Hypsilophodon*'s being arboreal. Later (1936*a*) he pointed out that this armour was insufficient to protect *Hypsilophodon*

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* Swinton (1936 : 575) actually cited 'the more proximally placed radial crest' but no such structure was mentioned in his description (: 563–564) and, from the context, it is apparent that he meant the delto-pectoral crest. He mentioned (: 564) that the deltoid crest was more proximally placed than in the other genera, 'a point which will be considered further later'.

from contemporary carnivores and that it was probably not fleet enough to escape by running. He suggested that, in times of danger, *Hypsilophodon* climbed up into the trees where, in addition, it obtained its food.

More recently, Swinton (1962 : 24) wrote that 'it has been thought that the lengths of the fingers and toes of *Hypsilophodon* indicate that it could climb trees ; but this is probably a wrong assumption, though the animal could no doubt run up sloping trunks'. However, the accompanying reconstruction (pl. 9) showed *Hypsilophodon* well up a tree. Romer (1956 : 414) noted that in '*Hypsilophodon*, digit I diverges from its neighbours, as in *Thescelosaurus*, but is relatively long, with digital articulations suggesting a clutching power and hence habits possibly somewhat arboreal in nature for ancestral ornithischians'. More recently (1966 : 158) he noted that 'some structural features of *Hypsilophodon* suggest arboreal habits comparable to those of the tree-kangaroo of Australia'. These features, which have been mentioned above, can be summarized according to the region concerned as follows :

b) *Summary of the purported anatomical evidence that* Hypsilophodon *was arboreal*

- i) Grasping capabilities of the pes :
  - A) Strong flexural ability of the long toes and the long, thin, pointed and curved unguals.
  - B) Opposability of the hallux.
- ii) Grasping capabilities of the manus :
  - A) Length of the middle three digits.
  - B) Long, thin, pointed and curved unguals.
- iii) Wider range of brachial movements possible :
  - A) Humerus longer than scapula.
  - B) More proximal position of the deltopectoral crest of the humerus.
  - C) Medial position of the articular head of the humerus.
- iv) Nature of fore-arm with a marked bowing of the radius which, by analogy with *Dendrolagus*, is an arboreal adaptation, and which is not found in other dinosaurs.
- v) Rigid tail an aid to balancing.
- vi) Dermal armour only light and therefore inadequate as a protection from ground-living predators.
- vii) Limited running capabilities on the ground resulting from the structure of the hindlimb :
  - A) Sharp and strongly arched claws hampered movements.
  - B) Metatarsus not elongated as in truly cursorial forms.
  - C) The low position of the insertion of leg muscles on the fourth trochanter of the femur.

c) *Discussion of this evidence*

i) GRASPING CAPABILITIES OF THE PES

Abel (1912), when discussing his reconstruction of the foot (see Text-fig. 63), considered that the pose shown was natural because the nature of the articular surfaces permitted no other reconstruction. If this is correct then *Hypsilophodon* must have found it rather difficult to change its grip! However, the nature of the flexural abilities of the toes as determined by the articular surfaces, together with the lengths of the phalanges and the nature of the unguals, is no different in *Hypsilophodon* from what it is in the hypsilophodontids *Thescelosaurus* (see Gilmore 1915), *Parksosaurus* (see Parks 1926), *Dysalotosaurus* (see Janensch 1955, 1961) and the psittacosaurid *Psittacosaurus* (Colbert 1962, fig. 29). Outside the Ornithischia the digits of the feet are also very similar in most pseudosuchians (*Hesperosuchus*, see Colbert 1952), coelurosaurs (*Coelophysis*, Colbert 1962, fig. 8) and prosauropods (see comparison of feet of *Hypsilophodon* and *Anchisaurus* in Galton, 1970*a*, *Plateosaurus* in von Huene 1926). Even in the relatively short phalanges of larger dinosaurs the articular surfaces are still very similar; the unguals of *Camptosaurus* (see Gilmore 1909) and *Iguanodon* (see Hooley 1925) are moderately curved. However, the unguals of ornithomimids, which are regarded as cursorial dinosaurs *par excellence* (Osborn 1917, Colbert 1962, Romer 1956, 1966) are even more pointed, longer and thinner than those of *Hypsilophodon*. It is apparent that digits II to IV of the foot of *Hypsilophodon* closely resemble those of many other dinosaurs.

Only in specimen R196 are the feet well preserved with articulated phalanges and Abel (1912) clearly based his reconstruction on this specimen. As drawn (Text-fig. 63) metatarsal V is too long and the length and proportions of most of the phalanges are incorrect. However, the first metatarsal is shown closely applied to the side of metatarsal II and its first phalanx is quite accurately drawn from the right foot. An examination of the complete first digit of the left foot (Pl. 2, fig. 3) shows that the curved ungual should point ventrally. The correctness of this articulation is confirmed by comparing the distal articular end of the first phalanx with the corresponding region on digits II to IV (see Text-fig. 58). Consequently Abel (1912) in his reconstruction rotated the first ungual through 180 degrees so that it pointed dorsally instead of ventrally.

In R196 the first metatarsal is closely applied along its whole length to metatarsal II as drawn by Abel (1912) and Heilmann (1926). Swinton (1936) stated that Heilmann (1926 : 162) showed the end of metatarsal I diverging distally. However, it would appear that Swinton had looked at figure 115 (4), that of *Anomoepus* (foot reconstructed from footprints from the Upper Triassic of the Connecticut Valley, in which metatarsal I indeed diverges), rather than figure 115 (3) of *Hypsilophodon*, in which metatarsal I is shown closely applied to metatarsal II. Swinton noted that in the human hand some opposable action of the thumb is still possible even when the first metacarpal is kept closely approximated to the second. However, metacarpal I cannot be closely approximated to metacarpal II because there are muscles that get in the way. In addition, this opposability of the thumb is rather ineffective and is merely a result of the angle of the distal articular condyle of metacarpal I. With the wrist held horizontally this angle is about 45 degrees to the horizontal so that the phalanges of digit I can be moved towards those of the adjacent digit (i.e. ventro-laterally). In *Hypsilophodon* the plane of the condyle of metatarsal I is approximately horizontal so that the phalanges of digit I can move only ventrally or even slightly ventro-medially. The fifth digit of the human hand would provide a better analogy. In both cases no amount of distal divergence will make the digit opposable, only a considerable amount of ventral rotation of metacarpal V (or metatarsal I).

The first metatarsal of *Hypsilophodon* has a greatly compressed proximal portion which wraps round on to the dorso-lateral surface of the second metatarsal (see description and Text-fig. 58). In addition, there is practically no proximal articular surface. There is no isolated first metatarsal but it would closely resemble that of *Parksosaurus* (Parks 1926, figs. 15, 16). In both *Hypsilophodon* and *Parksosaurus* the form of the first metatarsal shows that any lateral movement away from the second metatarsal was impossible and, as a result, ventral rotation was out of the question. Consequently the most important argument for regarding *Hypsilophodon* as a tree-climber, the opposability of the hallux, is based on misinterpretations of the material.

ii) GRASPING CAPABILITIES OF THE MANUS

The ungual phalanges of the manus resemble those of the pes but Swinton (1936 : 676) exaggerated slightly in describing them as long and thin. He also mentioned the 'comparatively elongated three middle digits' while, as can be seen in Text-fig. 41, the fourth digit is in fact quite short. Although Abel, Heilmann and Swinton argued that the hallux of *Hypsilophodon* was opposable, they did not discuss the possibility that the fifth digit of the hand was opposable as may have been the case (see page 126).

The hand of *Hypsilophodon* could probably grasp objects very well, provided that they were small. The manus is much smaller than the pes (Text-figs. 41, 58, both from specimen R196) with metacarpal III, the longest in the hand, being shorter than the rudimentary metatarsal V. The small size of the manus would have restricted its usefulness as an aid in climbing, but a grasping hand is not confined to arboreal forms. The fifth digit of *Iguanodon* bears phalanges (more than any other digit) and metacarpal V, which has a concave proximal surface, is set at quite an angle to metacarpal IV (Hooley 1925). The fifth digit of hadrosaurs is similar (Parks 1920, Lull & Wright 1942). Consequently the fifth digit, which was certainly adapted for grasping, may have been opposable, even though these ornithopods (length 6–9 m) were much too large to climb trees. The coelurosaurs *Ornitholestes* and *Struthiomimus* are supposed to have had an opposable first digit (Osborn 1917) ; and the hand of the coelurosaur *Coelophysis*, with its long second and third digits, was probably also a good grasping organ (Colbert 1962). The coelurosaurs are generally regarded as cursorial forms (Colbert 1962, Romer 1966).

iii) WIDER RANGE OF BRACHIAL MOVEMENTS POSSIBLE

Swinton (1936) believed that the humerus of *Hypsilophodon* was longer than the scapula. However, he based this view on specimen R5829, in which both scapulae are unnaturally shortened because of the loss of their dorsal ends. In R5830, R196 and R192 the humerus is about the same length as the scapula (see Table II). Swinton also pointed out that the delto-pectoral crest was rather proximal in position in *Hypsilophodon*. However, its position in *Dysalotosaurus* (see Janensch 1955) and

Iguanodon atherfieldensis (see Hooley 1925) is almost identical. Lastly, Swinton thought that the head of the humerus was rather medial in position. However, differences in the position of the head in *Hypsilophodon*, *Thescelosaurus* (Sternberg 1940, fig. 14b, Galton, in press *a*), *Camptosaurus* (Gilmore 1909, fig. 26) and *Iguanodon* (Hooley 1925, fig. 7 – IV) are minimal and lack any real significance. It is therefore concluded that the range of brachial movements was not greater developed in *Hypsilophodon*.

iv) LARGE FORE-ARM SPACE

The radius and ulna of *Hypsilophodon* are slender but the degree of development of the fore-arm space is comparable to that of *Thescelosaurus*, *Dysalotosaurus* and *Camptosaurus nanus* ; the radius and ulna are very similar in form in the first two genera. The fore-arm space of *Iguanodon atherfieldensis* is also quite well developed. This space is therefore not uniquely large in *Hypsilophodon*, and it is not true that *Hypsilophodon* differs from all other dinosaurs in the same way that the arboreal *Dendrolagus* differs from ground-living kangaroos.

v) RIGID TAIL AS A BALANCING ORGAN

The ensheathing tendons must have made the posterior two-thirds of the tail rather rigid. They would have enhanced the effect of the vertical articular surfaces of the pre- and post-zygapophyses of the caudal vertebrae from about the tenth vertebra onwards. The attitude of these facets must have restricted movement laterally while the ossified tendons would have also restricted it dorso-ventrally. The base of the tail was much more flexible because the absence of tendons in this region is probably natural and the articular planes of the zygapophyses are at about 45 degrees to the vertical. However, the distal part of the tail is also ensheathed in ossified tendons in the other hypsilophodontids in which this region is well preserved, namely *Parksosaurus* and *Thescelosaurus*. The tail is ensheathed in several dinosaurs, including two from the Lower Cretaceous of Montana – an ornithopod (Ostrom, personal communication) and a theropod (*Deinonychus*, Ostrom 1969). *Hypsilophodon* is thus not unique in having a rigid tail, which would have been useful while running on the ground. The rigidity would have increased the efficiency of the tail as a dynamic stabilizer when the animal rapidly changed its direction (see discussion for *Deinonychus* in Ostrom 1969 : 68).

vi) DERMAL ARMOUR

Hypsilophodon is the only ornithopod in which any trace of armour has been found ; other ornithopods were even less well protected against predators.

vii) LIMITED RUNNING CAPABILITIES

The ungual phalanges of *Hypsilophodon* do not differ from those of most other dinosaurs. In order to discuss the proportions of the hindlimb of *Hypsilophodon* the ratios for other Ornithopoda are given in Table V. Those for certain Saurischia are also given, together with those for perissodactyls and artiodactyls considered by Gregory (1912) as cursorial.

The ratio of tibia : femur in *Hypsilophodon* is, together with that of its closest relative *Parksosaurus*, higher than in any other post-Triassic ornithopod. Indeed the tibia is longer than the femur in only a few ornithischians. This ratio is higher only in the saurischian *Struthiomimus* and in a few of the cursorial perissodactyls and artiodactyls. The ratio of the third metatarsal : femur is larger in *Hypsilophodon* than it is in any other ornithischian. However, it is low in comparison with *Struthiomimus* and *Coelophysis* and, amongst the cursorial ungulates, the ratio is lower only in *Eohippus*. The ratio of the combined length of the tibia and third metatarsal : femur indicates the degree of elongation of the lower segment of the leg. This ratio in *Hypsilophodon* (at 1·78 or 1·73) is higher than in any other post-Triassic ornithischian while in the saurischians it is higher only in *Coelophysis* (1·67 or 1·86) and *Struthiomimus* (1·90 or 1·99). However, coelurosaurs and more especially the ornithomimids are generally regarded as the dinosaurs most highly adapted for fast running (Osborn 1917, Colbert 1962, Romer 1956, 1966). This last ratio shows that amongst the Ornithischia *Hypsilophodon* was the best adapted for fast running. It falls in the middle range of the cursorial species listed by Gregory (1912) and is better adapted than *Eohippus*, *Mesohippus*, the race-horse and *Tragulus napu*.

The ratio of X : femur, where X is the minimum length between the neck of the femur and the distal surface of the fourth trochanter (Text-fig. 1f), is certainly lower in most Theropoda than it is in *Hypsilophodon* ; the fourth trochanter is closer to the head even in *Gorgosaurus*. With a low value for this ratio the caudifemoralis longus muscle has a smaller moment arm and a faster action. This is an adaptation that is important in cursorial animals (Gregory 1912) and, although the fourth trochanter is relatively low in *Hypsilophodon*, it is even lower in other ornithischians that were less well adapted for fast running.

It is concluded that *Hypsilophodon* was not specifically specialized for an arboreal mode of life but, on the contrary, was cursorial. Individuals may occasionally have gone up into the trees but this would have occurred no more frequently than in any other small (up to 2·28 m long) and active dinosaur (see below : 149).

IX. GENERALIZED FEATURES OF *HYPSILOPHODON*

Hypsilophodon has been correctly regarded as a very primitive ornithopod and the more noteworthy features will be considered briefly with comments on the position in other ornithopods. Unfortunately the number of genera with which comparisons can be made is necessarily limited by inadequacies in the fossil record or in the published accounts. The relationships of *Hypsilophodon* are summarized below (: 150).

The snout is short, the skull deep with a large orbit and there is a supraorbital (Text-fig. 3) as in *Heterodontosaurus* (see Crompton & Charig 1962, Galton 1970*a*), *Parksosaurus* (Parks 1926, Galton in press), *Dysalotosaurus* (Janensch 1955) and in

TABLE V

Hindlimb measurements and ratios of dinosaurs and cursorial ungulates
(Measurements in mm)

	F	T	MT	$\frac{X}{F}$	$\frac{T}{F}$	$\frac{T + MT}{F}$	$\frac{MT}{F}$	$\frac{MT}{T}$
ORNITHISCHIA								
Hypsilophodon foxii R5830	101	118	63	0·42	1·17	1·79	0·62	0·53
R196	151	(178)	84	0·43	1·18	1·73	0·56	–
R5829	200	238	–	0·43	1·19	–	–	–
Forelimb R196	(105)$^{\mathrm{H}}$	(88)$^{\mathrm{U}}$	(24)$^{\mathrm{MC}}$	–	(0·84)	(1·07)	(0·23)	(0·26)
Parksosaurus warreni[1]	270	320	151	0·49	1·18	1·74	0·56	0·47
Dryosaurus altus[2]	353	394	185	0·47	1·10	1·64	0·52	0·47
Dysalotosaurus[3]	–	–	–	0·45 0·47	1·10	1·69	0·59	0·54
Psittacosaurus[4]	162	179	93	0·50	1·10	1·68	0·57	0·52
Protiguanodon[4]	158	167	89	0·50	1·06	1·59	0·56	0·53
Stegoceras (Tröodon) validus[5]	222	220	85	–	0·99	1·33	0·38	0·38
Camptosaurus nanus[6]	242	231	97·5	0·54	0·95	1·31	0·40	0·42
Thescelosaurus edmontonensis[7]	320	290	–	–	0·90	–	–	–
Kritosaurus incurvimanus[8]	1045	943	363	0·54	0·90	1·24	0·35	0·38
Iguanodon atherfieldensis[9]	678	595	240	0·48	0·88	1·23	0·35	0·40
Thescelosaurus neglectus[10]	355	300	127	0·44	0·84	1·20	0·36	0·42

TABLE V (*cont.*)

	F	T	MT	$\frac{X}{F}$	$\frac{T}{F}$	$\frac{T + MT}{F}$	$\frac{MT}{F}$	$\frac{MT}{T}$
SAURISCHIA								
Ornithomimus brevitortius[11]	390	483	293	–	1·24	1·99	0·75	0·60
Struthiomimus altus[12]	480	540	370	0·33	1·12	1·90	0·77	0·68
Coelophysis bauri[13]	118	135	84	–	1·14	1·86	0·71	0·62
	209	224	126	–	1·07	1·67	0·60	0·56
Gorgosaurus[14]	1040	1000	594	0·39	0·96	1·53	0·57	0·59
Ornitholestes hermanni[12]	207	159	117	–	0·77	1·33	0·57	0·73
Anchisaurus[15]	210	147	98	0·41	0·70	1·17	0·47	0·66
Plateosaurus[16]	680	500	240	0·52	0·74	1·09	0·35	0·48
MAMMALIA								
Perissodactyla[17]								
Eohippus sp.	162	162	82	–	1·00	1·51	0·50	0·50
Mesohippus sp.	178	193	121	–	1·08	1·76	0·68	0·63
Neohipparion whitneyi	249	293	252	–	1·17	2·19	1·01	0·79
Equus caballus (race horse)	392	363	288	–	0·92	1·66	0·73	0·79
Artiodactyla[17]								
Tragulus napu	94	103	62	–	1·09	1·75	0·66	0·60
Odocoileus hemionus	253	295	255	–	1·16	2·13	1·00	0·86
Gazella dorcas juv.	140	176	132	–	1·25	2·20	0·81	0·75
Antilope cervicapra	183	223	183	–	1·21	2·34	1·00	0·82
Antilocapra americana	210	260	218	–	1·23	2·28	1·03	0·84

Abbreviations:F, femur; H, humerus; MC, third metacarpal; MT, third metatarsal; T, tibia; U, ulna ; X, fourth trochanter index, see Text-fig. 1f. Sources of measurements: 1, Parks 1926 and Edmund, personal communication; 2, Yale Peabody Museum No. 1876, 1884 for MT from a slightly smaller individual; 3, Janensch 1955; 4, Osborn 1924; 5, Gilmore 1924; 6, United States National Museum No. 2210; 7, Sternberg 1940; 8, Parks 1920; Hooley 1925; 10, Gilmore 1915; 11, Sternberg 1933; 12, Osborn 1917; 13, Colbert 1964; 14, Lambe 1917; 15, Lull 1953; 16, von Huene 1926; 17, Gregory 1912, all genera listed as cursorial.

the skulls referred to *Laosaurus* and *Dryosaurus* by Gilmore (1925). The snout is longer with a more elongated tooth row and a proportionally smaller orbit in *Camptosaurus* (Gilmore 1909), *Iguanodon* (Hooley 1925) and hadrosaurs (see Lull & Wright 1942. (Hadrosaurs will be mentioned only when there is a difference from *Iguanodon*.)

The posterior process of the premaxilla is short and slender as in thecodontians and, since it does not contact the prefrontal or the lachrymal, the nasal is not completely separated from the maxilla. This is also the case in *Parksosaurus* where this process, though short, is broad and has a good suture with the maxilla. The posterior process is long and contacts the prefrontal and lachrymal in *Heterodontosaurus, Dysalotosaurus, Camptosaurus* and *Iguanodon*.

In thecodontians the antorbital fenestra is large (Romer 1956) as was also the case in *Heterodontosaurus*. It is quite large in *Hypsilophodon* but is much smaller in *Laosaurus* and *Dryosaurus* and practically non-existent in *Parksosaurus, Dysalotosaurus, Camptosaurus* and *Iguanodon*. The quadratojugal was not excluded from the margin of the lower temporal fenestra by the jugal which, as a result, did not contact the quadrate. The jugal makes this contact and the quadratojugal is small in *Parksosaurus, Dysalotosaurus, Camptosaurus* and *Iguanodon*. The large size of the quadratojugal of *Hypsilophodon* (and the consequent reduction of the lower temporal fenestra) is a specialized feature.

Thecodontians had premaxillary teeth but these were lost in most ornithischians. They were retained in *Hypsilophodon, Heterodontosaurus, Thescelosaurus* (see Sternberg 1940, Galton in press *a*), *Stegoceras* (see Gilmore 1924), the ceratopsians *Protoceratops* and *Leptoceratops* (see Brown & Schlaikjer 1940) and the nodosaur *Silvisaurus* (Eaton 1960). The general form of the thickly enamelled side of the maxillary and dentary teeth resembles that of *Dysalotosaurus, Laosaurus* (see Marsh 1896), *Camptosaurus* and *Iguanodon*. There is a well-defined central ridge on each dentary tooth of *Hypsilophodon* as in *Laosaurus*. There is a strong central ridge on each maxillary tooth as well in *Dysalotosaurus* while in *Camptosaurus* the strong central ridge is restricted to the maxillary teeth. The thickly enamelled surface does not resemble that of *Heterodontosaurus, Fabrosaurus* (Ginsburg 1964), *Parksosaurus* or *Thescelosaurus*.

The lack of comparative data for the palate of thecodontians and of other lower ornithopods makes it difficult to recognize which characters of the palate of *Hypsilophodon* are generalized ; it would appear that the palatines and pterygoids of opposite sides did not meet at the midline.

In the vertebral column the neural spines are low as in *Dysalotosaurus* (see Janensch 1961) and they are progressively taller in the series *Parksosaurus, Thescelosaurus, Camptosaurus* (see Gilmore 1912) and *Iguanodon* (see Casier 1960). The first chevron is reduced to a nubbin while in *Dysalotosaurus* it is much longer but it is absent in *Thescelosaurus* and *Camptosaurus*.

Dermal armour is present in most thecodontians and, if the plates described by Nopcsa (1905) were correctly described (see page 102), then *Hypsilophodon* is the only ornithopod in which dermal armour has been reported. In stegosaurs and ankylosaurs dermal plates formed a strong armour.

In the pelvis the ilium is low as in *Parksosaurus*. The ilium is progressively deeper in the series *Thescelosaurus, Dysalotosaurus, Camptosaurus* and *Iguanodon*. The prepubic process of *Hypsilophodon* is not short as in the Triassic ornithischians *Fabrosaurus* and *Heterodontosaurus* (Crompton & Charig, personal communication) which probably represent the primitive ornithischian condition (see Galton 1970*a*). The rod-like prepubic process of *Hypsilophodon* resembles that of *Dysalotosaurus* and the anterior end is not expanded slightly as it is in *Thescelosaurus* (Galton in press *a*) and *Dryosaurus*. In *Camptosaurus* the prepubic process is deep and transversely flattened and this is even more marked in *Iguanodon*. The postpubic rod extends to the end of the ischium as in *Thescelosaurus, Dysalotosaurus* and *Camptosaurus* but it is much shorter in iguanodontids, hadrosaurs, psittacosaurids and ceratopsians. The obturator process of the ischium is on about the same position on the shaft as it is in *Thescelosaurus*. The obturator process is progressively more proximal in the series *Parksosaurus, Hypsilophodon, Dysalotosaurus, Camptosaurus* and *Iguanodon*. The distal part of the ischium is straight, flat and blade-like as it is in *Thescelosaurus* and *Parksosaurus*. In *Dysalotosaurus, Camptosaurus* and *Iguanodon* the ischium curves ventrally and the distal part is much more massive.

The manus has five digits with four phalanges on the third digit. The latter large number has been reported only in *Thescelosaurus, Psittacosaurus* (see Osborn 1924) and in *Protoceratops, Leptoceratops* and *Monoclonius* (Brown & Schalikjer 1940). The distal end of the femur has practically no anterior condylar groove. This groove is shallow in *Thescelosaurus* and *Parksosaurus* and becomes progressively deeper in the series *Dysalotosaurus, Dryosaurus, Camptosaurus* and *Iguanodon* while in hadrosaurs the edges meet above the deep cleft. Posteriorly the outer condyle is almost as large as the inner while in the above-mentioned genera the outer condyle is sheet-like and much smaller than the inner condyle. The cnemial crest of the tibia is small as in *Pisanosaurus* (see Casamiquela 1967) and *Dysalotosaurus*; it is much larger in *Parksosaurus, Thescelosaurus, Camptosaurus* and *Iguanodon*. In the pes a rudimentary fifth metatarsal is present as is the case in many other ornithischians.

At first sight it would appear that the cursorial adaptations of *Hypsilophodon* would be specialized rather than generalized features for ornithischians. However, the hindlimb of *Pisanosaurus* (Casamiquela 1967) from the Triassic Ischigualasto Formation of Argentina was probably more highly adapted for fast running than was that of *Hypsilophodon*. The tibia and third metatarsal of *Pisanosaurus* are both slender with a metatarsal to tibia ratio of 0·59 as against 0·53 for *Hypsilophodon*. The metatarsus of Triassic ornithischians from the Connecticut Valley (*Anomoepus, Sauropus*, see Lull 1953) was also very slender and elongated. Skeletons of *Fabrosaurus* and *Heterodontosaurus* collected from the Upper Triassic of southern Africa show that both were bipedal and were adapted for fast running (Crompton, personal communication; see below: 149). The proximal position of the fourth trochanter of the femur and the elongate tibia and third metatarsal of the hindlimb of *Hypsilophodon* appears to have been more generalized than any other post-Triassic ornithischian. Increased size in ornithopods appears to have been correlated with a more distal position for the fourth trochanter of the femur and a relatively shorter tibia and third metatarsal (Table V). This probably occurred several different times during the history of the group : in *Camptosaurus*, in the line to *Iguanodon* and the hadrosaurs (Rozhdestvenskii (1966), in the pachycephalosaurids and in *Thescelosaurus* (see Galton in press *a*). A reversion to quadrupedality and increased size occurred in the line close to *Psittacosaurus* that led to ceratopsians and in the lines to ankylosaurs and stegosaurs (Text-fig. 64).

From the above survey it is apparent that *Hypsilophodon* retained many features of a generalized nature for ornithopods and, as a result, probably for ornithischians as a whole. *Hypsilophodon* occurred too late in time to have been directly ancestral to ankylosaurs, stegosaurs and most of the ornithopods. Rozhdestvenskii (1966) has shown that hadrosaurs were probably derived from *Iguanodon* that, like the most primitive pachycephalosaurid (see Galton, 1971), was a sympatric contemporary of *Hypsilophodon*. The large size of the maxilla and quadratojugal would debar *Hypsilophodon* from the direct ancestry of *Parksosaurus*. Its skull is inadequately known but it is possible that *Thescelosaurus* may have been derived from *Hypsilophodon* by a broadening of the frontals, a decrease in the size of the orbit, the specialization of the teeth and by graviportal modifications of the postcranial skeleton (see Galton in press *a*). The psittacosaurids and ceratopsians could have evolved from a form that was similar to *Hypsilophodon* but in which the prepubic process was much smaller.

The restricted geographical and stratigraphical occurrence of *Hypsilophodon* is obviously the result of accidents of the fossil record as known to date. The discovery of representatives of this genus in Jurassic or even in Triassic rocks is a distinct possibility. If the Triassic ancestor had a larger antorbital fenestra, a smaller quadratojugal, a small prepubic process and a more massive postpubic rod then it would make a good structural ancestor for all Jurassic and Cretaceous ornithischians (see below : 149).

X. SUMMARY

Several articulated specimens of *Hypsilophodon* were prepared mechanically and with acetic acid. Although no new material was included this enabled a more thoroughly detailed description of the osteology to be made. Only a few features are still uncertain : the contacts between the palatine, parasphenoid and vomer ; the transverse relationships between the tooth rows of the maxillae and lower jaw ; the form of the complete fibula ; the number and shape of some of the carpal bones and of the phalanges of the fifth digit of the manus.

The femur of *Camptosaurus valdensis* Lydekker (1889) is referred to *Hypsilophodon foxii*. It represents the largest individual recognized to date and was from an animal of about 2·28 m.

The paroccipital process of *Hypsilophodon* appears to be formed completely by the opisthotic, with the exoccipital restricted to the lateral part of the occipital condyle. This is in contrast to the position in the hadrosaur described by Langston (1960) in which the exoccipital appears to form most of the paroccipital process. Contrary to previous reports the skull has a supraorbital and also a sclerotic ring which was presumably essential for accommodation as is the case in living sauropsids.

The areas of attachment of the jaw muscles were, apart from those of the M. pterygoideus dorsalis and ventralis, similar to those described by Ostrom (1961) for the hadrosaur *Corythosaurus*. In *Hypsilophodon* the dorsal part of the coronoid is covered with very well-developed insertion markings which support Ostrom's contention that the M. pseudotemporalis inserted there. The area on the braincase of *Corythosaurus* where the M. levator bulbi may have originated could be prootic and basisphenoid rather than laterosphenoid. Originally this surface was for the M. protractor pterygoidei but, when the skull became akinetic, this surface may have become free and was then occupied by the M. levator bulbi. The M. protractor pterygoidei probably originated on the equivalent area in *Hypsilophodon*, the skull of which was possibly mesokinetic, metakinetic and amphistylic. The large antorbital fossa opened posteriorly across the floor of the orbit and was presumably for the anterior part of the M. pterygoideus dorsalis, the pterygoideus D, or possibly for a postulated equivalent of the M. pterygoideus ventralis. The moment arm of the jaw adductor muscles was lengthened by the presence of a large coronoid process and an off-set articulation with the quadrate. The anterior part of the premaxillae and the predentary were enclosed by a horny beak which was used to crop plants. The mouth was probably small with a large cheek pouch lateral to the tooth rows. The maxillary teeth are thickly enamelled on the lateral surface and they curve medially while with the dentary teeth the reverse is the case. The thickly enamelled edge was much more resistant than the rest of the crown and formed a sharp leading edge to an obliquely inclined occlusal surface between which and its fellow there was a high shear component. The cutting effect of this edge was enhanced by the presence of serrations produced by vertical and parallel ridges on the thickly enamelled surface. The foramina on the medial surface of the tooth-bearing bones, one per tooth, represent a preadaptation for the development of high alveolar walls.

There is a surprising amount of variation, the most interesting of which is the presence of an additional sacral rib in some individuals; this supports the contention of von Beneden (1881) and Nopcsa (1918, 1929) that the sacral count can vary within an ornithopod species. The massive first sacral rib backed the slender pubic peduncle of the ilium and keyed that bone to the pubis. The humerus could have been held vertically and the fifth digit of the manus may have been well formed and opposable.

Hypsilophodon was clearly bipedal as shown by the fore- to hindlimb ratio, the hindlimb to trunk ratio and the restriction of cursorial adaptations to the hindlimb. The arguments advanced to put *Hypsilophodon* up in the trees, the position it occupies in every textbook, are reviewed historically and discussed under the separate regions of the body concerned. The first metatarsal was closely applied along all its length to the adjacent part of metatarsal II. The first digit of the pes was not opposable and all the phalanges closely resemble those of other dinosaurs. The relatively small size of the grasping manus would have restricted its usefulness in climbing and the fore-arm space was not uniquely enlarged by a bowed radius. The rigid tail with its sheath of ossified tendons would have been useful as an aid to balancing and steering while running on the ground. If dermal armour was present then this was more protection than possessed by any other ornithopod. Far from having limited running capabilities *Hypsilophodon* was the ornithopod most highly adapted for fast running if the ratios of the length of the femur : tibia, femur : third metatarsal and the position of the fourth trochanter mean anything. The values for the first two ratios fall in the middle range of those for the living ungulates that Gregory (1912) considered cursorial.

Although *Hypsilophodon* is from the Lower Cretaceous it has retained several features that may be generalized for ornithischians. The skull has a short snout with the retention of premaxillary teeth, the orbit is large and there is a supraorbital. The premaxilla has a short and slender posterior process that does not meet the prefrontal or lacrymal and, as a result, the maxilla meets the nasal. The quadratojugal is not excluded from the margin of the lower temporal fenestra by the jugal which, as a result, does not contact the quadrate. The neural spines are low, a first chevrons (rudimentary) is present and there may have been dermal armour. The manus has five digits with four phalanges on the third digit. The ilium is low, the postpubic rod is long and the distal half of the ischium is straight and blade-like. The fourth trochanter is placed proximally on the femur ; the distal end of the femur has practically no anterior intercondylar groove while posteriorly the outer condyle is almost as large as the inner condyle. The long tibia has a small cnemial crest. The fifth metatarsal is vestigial but the first to fourth are relatively elongate and the hindlimb is adapted for fast running. Structurally *Hypsilophodon* is quite similar to the hypothetical ancestor of the other ornithischians of the Jurassic and Cretaceous.

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NOTE

Several papers of related interest have appeared in the three years since the manuscript of this article was last revised. I have given a full discussion of the mode of life of *Hypsilophodon* (Galton 1971b) with figures illustrating the comparisons made above (: 133–137) and with stereo-photographs of the manus and pes of R196 in dorsal view ; an abstract of this paper appeared a little earlier (1971*a*). Two other papers (Galton 1973, Galton in press) include reconstructions of the skull of *Hypsilophodon* in ventral and dorsal view respectively and figures of the skull.

Thulborn (1970, 1971, 1972) gives a detailed description of the anatomy of the Upper Triassic ornithischian *Fabrosaurus australis* and, on the basis of my figures of

Hypsilophodon (Galton 1967), refers *Fabrosaurus* to the family Hypsilophodontidae. However, my concept of this family (Galton 1971*a*, *b*, 1972, 1973 in press, in press *a*) is not as all-embracing as Thulborn's (1970, 1970*a*, 1971, 1971*a*, 1972) who includes all cursorial ornithopods with premaxillary teeth plus *Thescelosaurus* (for genera see Thulborn 1972, fig. 14). I agree with Thulborn (1970, 1971, 1972) that the Upper Triassic *Fabrosaurus* is very similar to the archetypal ornithischian from which all other ornithischians were originally derived. Indeed, the skull of *Fabrosaurus* with its flat maxilla, slender dentary and marginally positioned maxillary and dentary teeth (see Thulborn 1970, Galton 1973) is so primitive that I place that genus (along with *Echinodon* Owen from the Lower Cretaceous of England) in a separate family, the Fabrosauridae (Galton 1972). This family resembled living reptiles in not having muscular cheeks. In all other ornithischians described to date there is a large space lateral to the tooth rows which is overhung by the maxilla and floored by the massive dentary ; it is presumed that this space was bordered by cheeks (as noted on page 121 for *Hypsilophodon*) which prevented the loss of food from the sides of the jaws, as would otherwise have occurred when resistant plant material was chewed repeatedly. I attribute the spectacular success of ornithischian dinosaurs, the dominant 'small to medium' (up to 10 m) sized terrestrial herbivores of the Jurassic and Cretaceous periods (about 125 million years), to their development of cheeks (Galton, 1972, 1973).

Thulborn (1970, 1970*a*, 1971, 1971*a*, 1972) refers *Heterodontosaurus* (as '*Lycorhinus*') to the family Hypsilophodontidae. *Heterodontosaurus* has cheek teeth with planar wear surfaces and there is a caniniform tooth on each premaxilla and dentary (see Crompton & Charig 1962, Thulborn 1970*a*). I consider (Galton 1972) that these dental specializations justify the retention of the family Heterondontosauridae, to which I also refer *Geranosaurus* and *Lycorhinus*. Thulborn (1970, 1970*a*, 1971, 1972) follows current practice in placing *Thescelosaurus* (graviportal, premaxillary teeth ; see Sternberg, 1940) in the family Hypsilophodontidae and referring *Dysalotosaurus* (cursorial, no premaxillary teeth ; see Janensch, 1955) to the family Iguanodontidae. These taxonomic assignments are based on the respective presence or absence of premaxillary teeth, but I consider that this criterion should not be used to determine which genera should be included in the family Hypsilophodontidae (see Galton 1972). The skull of *Dysalotosaurus* is very similar to that of *Dryosaurus* (cursorial, no premaxillary teeth) ; I therefore place both those genera in the Hypsilophodontidae and refer *Thescelosaurus* to the Iguanodontidae (Galton 1972, in press, in press *a*).

The cursorial ornithopods of conservative aspect should be referred to the family Hypsilophondontidae, diagnosed as follows :

Head small, snout short, orbits large ; no large rostral beak, no caniniform teeth, maxillary and dentary teeth inset (longitudinal recess to maxilla, massive dentary) and with randomly formed wear surfaces which are not all in the same plane ; distal part of hind limb elongate (Galton 1972, in press). The genera and specimens that I refer to this family are shown in the phyletic chart (Text-fig. 64) and the relationships shown are based largely on the form of the femur (for discussion of various aspects of this chart see Galton 1972, in press, in press *a*).

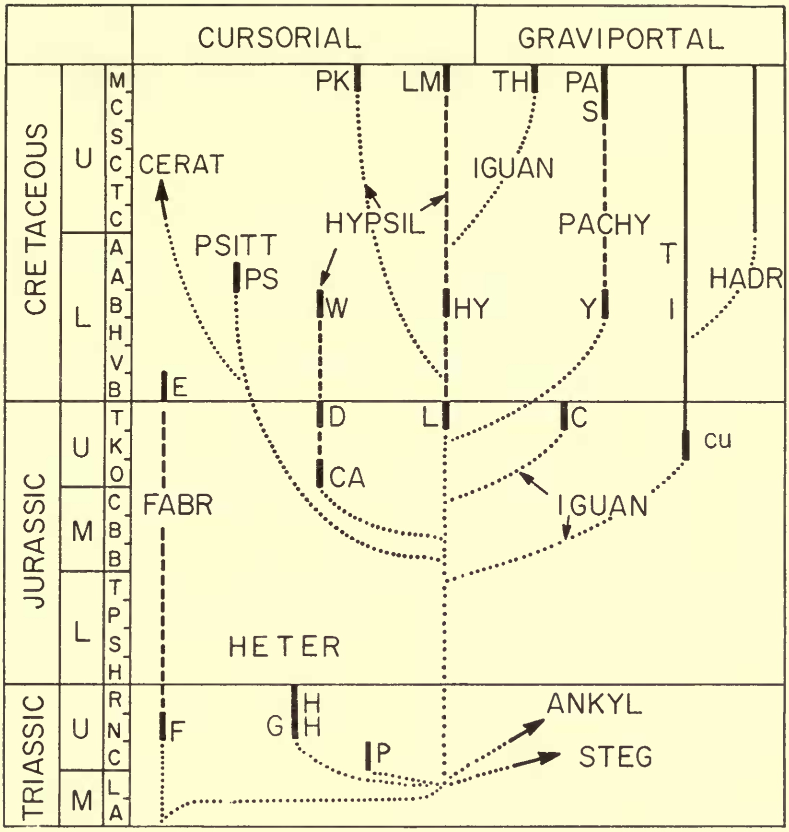

Fig. 64. Phylogeny of the Ornithopoda; modified from Galton (1972). Diagram to show phylogenetic relationships and the nature of the fossil record of lower ornithopods. The ages of the different genera are based on data in Charig (1967) and the stratigraphic distribution is by stages, the initials of which are given in the third column. Abbreviations: Classificationary units: ANKYL, Ankylosauria; CERAT, Ceratopsia; FABR, Fabrosauridae; HADR, Hadrosauridae; HETER, Heterodontosauridae; HYPSIL, Hypsilophodontidae; IGUAN, Iguanodontidae; PACHY, Pachycephalosauridae; PSITT, Psittacosauridae; STEG, Stegosauria. Genera: C, *Camptosaurus*; CA, '*Camptosaurus*' *leedsi*, R1993; CU, *Cumnoria* ('*Camptosaurus*') *prestwichi*, D, *Dryosaurus* and *Dysalotosaurus*: E, *Echinodon*; F, *Fabrosaurus*; G. *Geranosaurus* and *Lycorhinus*, H, *Heterodontosaurus*; HY, *Hypsilophodon*; I, *Iguanodon*; L, *Laosaurus*; LM, '*Laosaurus*' *minimus*; P, *Pisanosaurus*; PA, *Pachycephalosaurus*: PK, *Parksosaurus*; PS, *Psittacosaurus*; S, *Stegoceras*; T, *Tenontosaurus*; TH, *Thescelosaurus*; W, Wealden hypsilophodont (R184, R185, 36509, see above, p.7; to be described elsewhere); Y, *Yaverlandia* (Galton 1971). Actual fossil record of ornithopods indicated by ———; no fossil record indicated by - - - - - but genera in the same vertical line are closely related; postulated relationships indicated by ....

In this connection, however, it must be pointed out here that the Iguanodontidae as presently constituted are probably not a natural group, a monophyletic taxon. Text-fig. 64 shows that the 'family' comprises three lines of graviportal ornithopods arising independently from the Hypsilophodontidae: the Iguanodontidae *sensu stricto* (with *Cumnoria, Iguanodon* and *Tenontosaurus*), a line leading to *Camptosaurus*, and a line leading to *Thescelosaurus*.

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All anatomical terms refer to the species *Hypsilophodon foxii* Huxley.

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PLATE 1

Hypsilophodon foxii

FIG. 1. Skull R2477, dorsal view. Compare with Text-fig. 5B.
FIG. 2. Skull R2477, palatal view. Compare with Text-fig. 6A.
FIG. 3. Skull R2477, left lateral view. Compare with Text-fig. 4A.
FIG. 4. Skull R2477, right lateral view. Compare with Text-fig. 4A.
Scale line represents 5cm.

1

2

3

4

PLATE 2

Hypsilophodon foxii

FIG. 1. Skull R2477, dorsal view of palate and braincase. Compare with Text-fig. 5C.

FIG. 2. Skull R2477, medial view, compare with Text-figs. 4B, 60D.

FIG. 3. Pes R196, dorsal view of left pes.

FIG. 4. Femur R167, '*Camptosaurus valdensis*', from a large individual of *Hypsilophodon foxii*. a, anterior view ; b, posterior view.

Scale lines represent 5 cm.


2


1


4


3